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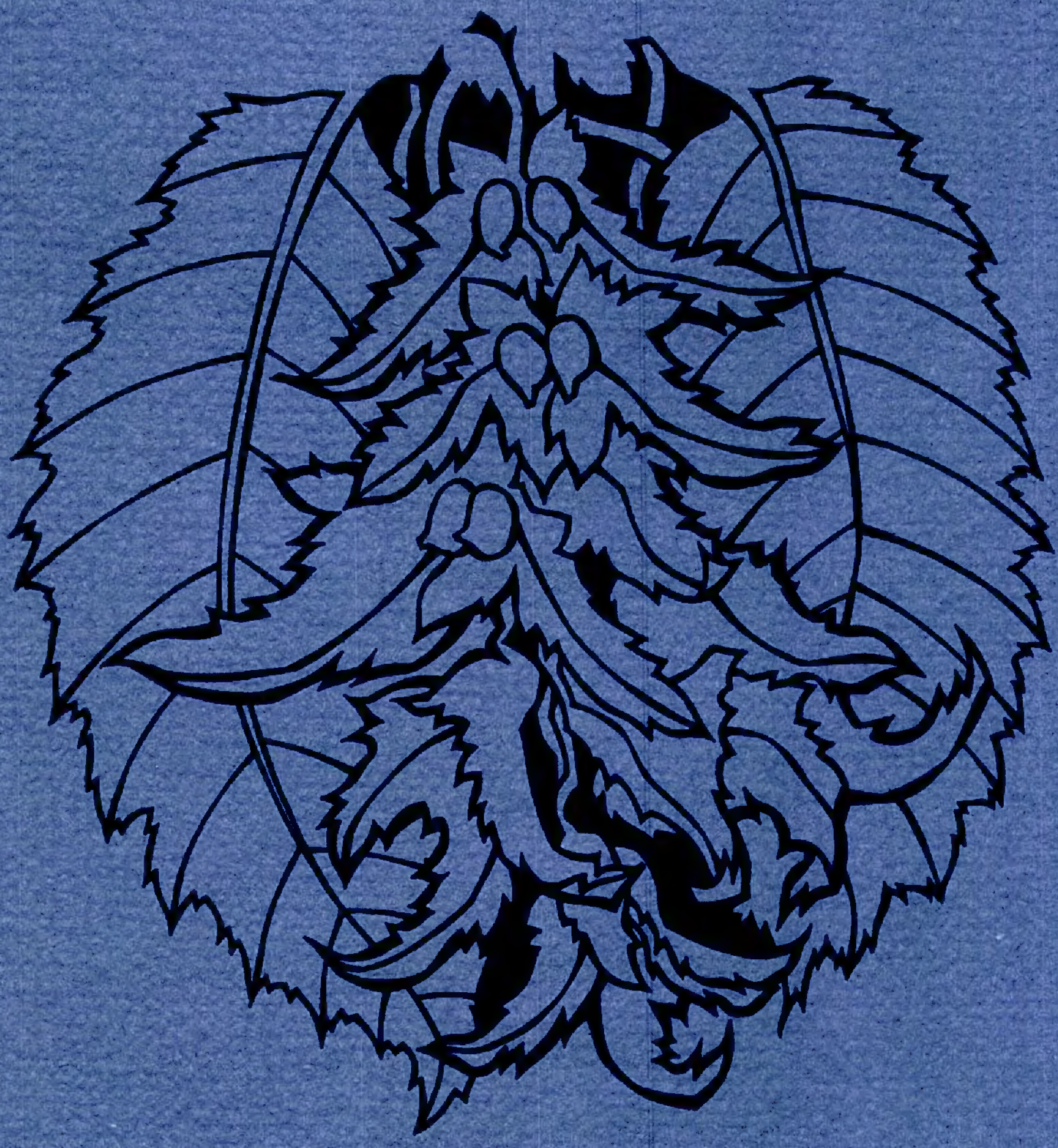

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COVER: The buds, leaves, and fruit of *Carpinus caroliniana* Walter, hornbeam or blue beech, form the basis of this year's cover design. An individual nutlet, together with its leafy, three-lobed wing, will appear on the offprints; a series of these was used in designing the device that appears on the back cover. The designs were all drawn by Karen Stoutsenberger from materials collected from plants growing in the Arnold Arboretum.

Widespread in the Northern Hemisphere, *Carpinus* L. (placed in the Betulaceae or alternatively in the Corylaceae or even the Carpinaceae), with upwards of 35 species, exhibits a disrupted Arcto-Tertiary distribution in eastern North America, Europe, Asia Minor, and in eastern Asia where the center of species diversity occurs. The only North American representative of the genus, *C. caroliniana* grows along the edges of streams and in wet, rich soils in forested areas from Nova Scotia and Quebec southward to Florida and westward into Minnesota, Iowa, Missouri, eastern Texas, and Oklahoma. Disjunct populations are known in mountainous regions of southern Mexico and in Central America.

The stems of *Carpinus caroliniana*, a small tree, have smooth, brownish- or bluish-gray, sinuate bark and an appearance reminiscent of those of beech trees (*Fagus* spp.). The wood, which is occasionally used for tool handles, is light brown to nearly white. Its growth habit, relatively small size, conspicuous infructescences, and foliage, which turns deep scarlet and orange to yellow in fall, combine to make this species an attractive native ornamental. — *S. A. S.*

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DAVID STURROCK
1893–1978
(photograph circa 1946)

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DAVID STURROCK (1893–1978) — MENTOR AND FRIEND

RICHARD A. HOWARD

FOR A PERIOD of ten years, 1936–1946, David Sturrock was superintendent of the Atkins Institution of the Arnold Arboretum at Soledad, north of Cienfuegos, Cuba. The garden and collection of tropical plants had been established by Edwin F. Atkins of Belmont, Massachusetts, as the Harvard Botanic Station for Tropical Research and Sugar Cane Research, and in 1932 was formally transferred to Harvard with an endowment and a lease of land from the Soledad Sugar Company. It was administered from Cambridge, at first by Dr. Thomas Barbour, Director of the Museum of Comparative Zoology, and later by Dr. Elmer D. Merrill, Director of the Arnold Arboretum. Both Barbour and Merrill believed that graduate students in biology at Harvard should have a personal experience in the tropics. To that end, a small grant of money, usually $200 to $300, enabled a thrifty student to travel to Miami or Key West by bus, train, or partway by boat; take a ferry to Havana and a train or bus to Cienfuegos; and spend one to three months in residence at "Soledad." Room and board charges were modest. Food was Cuban style and consisted of tropical products. The dormitory-type accommodations were at first in Harvard House and later in Casa Catalina. Both buildings had screened porches from which to watch the ever-busy sugar mill and plantations; to overlook the garden and see the sweep of the Trinidad-San Blas Mountains against the horizon; to read, press plants, and work up collections; to enjoy a "Sturrock special" before supper or at an evening bridge game; or to take part in the never-ending conversation on the biology of the tropics. The master of this community during my first visit as a student was David Sturrock, a lean, tanned man, usually dressed in white, who spoke Spanish with a Scottish accent — in contrast to the pure Castilian Spanish of Teodoro, the Spanish-born cook, or the Cuban-dialect Spanish of Manuelo, the houseboy. Sturrock ran a tight ship, making it clear more than once that the money awarded to us for Cuban adventure was money from his budget that might better have been spent on the operations of the garden. We were welcome if we demonstrated a use of the resources assembled, and unwelcome if this

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was only a vacation. Yet it was his influence that directed the research of several students to lifetime investigations in the problems of the Antilles.

David Sturrock was born in Lanark, Scotland, October 28, 1893, one of the eight children of William and Mary Dunn Sturrock. His father, a forester by profession, was the manager of a nursery of fruit and timber trees, with a few ornamentals. Formal schooling under the British system of that time ended at the age of fourteen, and David went to work in a nursery, handling seeds, propagating plants, shipping, planting on contract, pruning, budding, and learning business methods, personnel relations, and plants in the process. At one time he considered an offer from a local businessman to finance his education at Kew Gardens. Local men with more experience advised him against being molded in the Kew fashion, doing only what he was told, and suggested that it would be better instead to learn variety in plants and procedures and to think for himself. He later regarded that as good advice, for further experience in other nurseries broadened his background in the care and use of woody plants.

One of his older brothers, who had emigrated from Scotland and now managed a nursery in Miami, offered him employment in the United States. David saved his passage fare plus the $50 reserve then required by the United States Immigration Service and landed in New York in September, 1913. He was disturbed at the lack of care and appreciation of plants he saw in Central Park and the New York Botanical Garden and without reluctance traveled south to join his brother's business. His initial assignment in Florida was to locate sources of seeds and scions of ornamental plants useful in landscaping new homes. Without prior knowledge or prejudice, he chose plants from their appearance. Then the company received a contract to landscape the property being developed for the wealthy James Deering. Now known as Viscaya, this land is a current showplace for tourists in the Miami area. Expenditures seemed unlimited, and very large plants were moved with much labor. Many were brought in from the Bahamas, but to locate additional plants Sturrock was sent to Cuba, where he roamed the island searching for ideal specimens and learning the soil, the natural vegetation, and the farming methods. In the process he met Adolph van Hermann, who owned a small nursery. When the Viscaya project was completed, Sturrock resigned from his brother's firm, moved to Cuba in 1915 on his twenty-second birthday, and accepted the management of Van Hermann's nursery. Van Hermann's botanical interests were both practical and scientific. He collected herbarium specimens which were sent to the New York Botanical Garden, and Sturrock was exposed to the methods of botanical field work. Van Hermann had a pioneer planting of Mulgoba mango which proved to be Sturrock's introduction to a plant he was to propagate, breed, and study for the rest of his life. Van Hermann was also concerned with afforestation of some estates, and Sturrock had the task of developing a timber tree nursery as well. In satisfying his employer's many interests, Sturrock visited the agricultural experiment station in Santiago de las

Vegas and met Dr. Juan T. Roig, the prominent Cuban botanist with whom he shared interests for many years.

In 1915 David Sturrock, a house guest of the Van Hermanns, was invited to join them at a house party given at Christmas by Professor and Mrs. Franklin Sumner Earle in Herradura. Professor Earle had been sent to Cuba by the U. S. Department of Agriculture after the Spanish-American War to establish an agricultural experiment station. He had also served as the president of the Botanical Society of America and was a specialist in diseases of sugar cane. It was at that party that David Sturrock first met Ruth Earle, whom he married in May, 1918. Their sixtieth wedding anniversary was celebrated six weeks before his death.

David Sturrock had applied for United States citizenship in 1913, and within the five-year grace period returned to Miami. The United States was engaged in the first World War, and by enlisting and taking an oath of allegiance Sturrock obtained American citizenship immediately. He served in a medical service unit in France. After the armistice he returned to Cuba, where he accepted a position with the Hershey Sugar Company, reforesting land and developing a nursery for the sale of ornamentals and fruit trees while managing the production of tropical fruits and vegetables that were exported to New York.

Mr. Hershey had a sincere interest in the Cuban people and chose David Sturrock to organize a school for orphans from his Central to be trained in agricultural methods. The students had to be at least eight years of age, and by age fifteen were to be discharged from the school and given a position with the sugar company. Thirty boys were selected for the program, which included experience with crops and animals on the 1,000-acre farm during the mornings, and classes with a resident teacher in the afternoons. The school, known as the Hershey Agricultural School at Aguacate, Cuba, closed for financial reasons in the depression year of 1929.

At this point, David and Ruth Sturrock returned to Florida with their three children. David's older brother and his parents now lived in West Palm Beach, and there David reestablished his nursery and landscaping business as a means of supporting a desire to select and hybridize better varieties of mangoes for Florida. He acquired the Philippine mango from the Earles' property in Cuba, additional mangoes from the work of Edward Simmonds at the Federal Experiment Station in Miami, and mulgobas from the Van Hermann and Hershey estates. From these stocks David developed an inventory of small plants. Then in 1936 he received a visit from Thomas Barbour, who asked him to succeed the retiring superintendent at Soledad, Mr. Robert Grey. The salary was not much, but the opportunity was large and David accepted. His family remained in West Palm Beach during the school year and joined him in Soledad during the summers.

Managing the operation at Soledad was a job for an optimist. Its living collections had been decimated by a hurricane the previous year. Its directives were not clear. The budget was prepared and administered through two or more individuals in Cambridge, who visited Soledad on oc-

casion during the winter months. The donors' land and activities surrounded the garden area and posed problems, especially when oxen, cattle, and horses broke into the garden and nursery. The land available was largely rocky outcrops, unsuitable for growing sugar cane or for pasture, and water sources were inadequate. The Cuban government, under the Batista regime, hardly understood the purposes of the garden but controlled, through legislation, the labor and much of the daily operation.

Cuba at that time had a one-crop agricultural economic system based on sugar cane. Under Robert Grey the garden's research effort had been largely in cane. However, the Atkins family had been interested for many years in finding other crops that could aid the economy but that would not compete for labor during the cropping period. Sturrock had a special interest in fruits and timbers, and the garden had the potential of introducing new plants for trial. The seed lists sent to the Arnold Arboretum from botanical gardens throughout the world were used to request seeds, and Sturrock developed a list of seeds from Soledad plants that could be offered in exchange. An inventory of the plants in the garden had been prepared, and under Sturrock's direction, the total holdings rose to 124 families, 857 genera, and 4396 species. It was certainly the best collection of labeled and mapped plants for convenient study anywhere in the American tropics. With the nearby natural vegetation of seacoast, mangrove, serpentine savanna, and mountains, as well as the large Zapata swamp, it was an ideal place in which to teach and learn. Harvard House contained a laboratory and darkroom, a small but adequate library, and a small herbarium based largely on my own collections and those of John George Jack of the Arnold Arboretum. A publication series was started. For a few years a regularly scheduled Harvard class, Biology 215 (Plants of the Tropics), was conducted at Soledad. Visiting professionals were numerous, and Sturrock always did his best to accommodate their needs — from horses for local transport to vials and packaging material for their collections.

The major problem at Soledad, however, remained the financial base, never adequate for the potential of the garden and eventually unable to support even restricted operations. During the years of World War II, the staff, in a patriotic effort, devoted its attention to plants of economic significance in a wartime economy. Two hundred bushels of seeds of *Hevea brasiliensis*, the rubber tree, were received, germinated, and planted. Four hundred pounds of the lightweight seed of *Cryptostegia*, the Madagascar rubber vine, were collected from this milkweed relative and shipped to U.S.D.A. projects in Haiti. One thousand seedlings of *Tectona grandis*, the teak, were planted. Evaluations were made of fiber sources in the arid land collection called "Utah." As a result, maintenance of the garden was reduced, and many plants suffered. The war increased the problems of supplies and equipment. When it was decided in Cambridge in 1945 to cut the Soledad labor force in half, Sturrock and Harvard came to a parting of ways.

Sturrock returned to West Palm Beach but continued his work in Cuba

by developing forest plantings for several sugar companies, which he supervised until Castro gained control of the island. In Florida Sturrock acquired additional groves of mangoes for further intensive hybridization. Although the fruit was well known, the biology of the plant was not. Conventional hand-pollination did not work. Fruit-set was low, and fruit abortion and drop were high. Applications of hormones, successful in other crops, were not successful with mangoes. Seeds were shown to be mono- or polyembryonic, and gametic and nucellar plants developed with different characteristics. Sturrock worked out a method of inarching seedling plants by suspending a container-grown seedling within the branches of an adult tree when conventional grafting methods failed. All of these studies resulted in publications by David Sturrock or his son, who chose the mango as subject for his Ph.D. thesis. Eventually David selected and patented two first-generation hybrids. In 1956 a cross of the 'Edward' ♀, a monoembryonic plant, and 'Pico' ♂, a polyembryonic type, produced the patented 'Duncan', a monoembryonic plant, as well as the equally good but unregistered 'Mekong' and 'Wester', both polyembryonic. Using the monoembryonic 'Edward' as the female parent, and 'Kent', also monoembryonic, as the male, Sturrock selected and patented 'Young', a monoembryonic type. Mangoes take between four and seven years to flower and set fruit, and third-generation crosses made in 1966, 1967, and 1968, with the monoembryonic parents 'Haden' and 'Duncan', produced the excellent 'Sturrock' (patent pending) and about thirty other selections still under evaluation. A visit to the Sturrocks' home during these years of mango testing was a gustatory delight. Guests were asked to examine, test, and evaluate not one but many fresh mangoes in season, and frozen pulp at other times.

His interest in tropical fruits was wide. While at Soledad, and later in West Palm Beach, David and his wife grew and tested hundreds of tropical fruits, working out methods of preparation and preservation. The first publication of the Atkins Institute of the Arnold Arboretum was *Tropical Fruits for Southern Florida and Cuba and Their Uses*. This became known as "the jelly book" and is widely quoted today in the literature of tropical botany. Recipes prepared by the Sturrocks appeared in most of his writings, and a later publication, *Fruits for Southern Florida*, appeared serially in the *Stuart News* before publication as a hardcover book. This has been reprinted once and is scheduled for an additional printing in 1979. His favorites, as I recall with pleasure, were a sherbet made of *Carissa macrocarpa*, a jelly of *Carissa karandas*, and, for eating out of hand (second only to mangoes), *Myrciaria floribunda* (jaboticabá).

In cooperation with Dr. Edwin A. Menninger, Sturrock compiled his notes on tropical ornamental plants. The volume *Shade and Ornamental Trees for South Florida and Cuba* was originally published in serial form in the *Stuart News*. This was the first volume for Florida that paid attention to salt-resistant trees for exposed coastal sites, the areas of deep, overdrained sands, the shallow areas over rock, and the poorly drained areas inland. It is one of the few volumes in tropical and subtropical hor-

ticulture that emphasize the ecology of the planting site. Again, his wife contributed to his work, this time by supplying the drawings of the plants.

Sturrock's work with potential timber trees climaxed in perhaps his least-appreciated volume, *Trees for Southern Florida: A Plea for Afforestation*, which was published by the Central and Southern Florida Flood Control District in West Palm Beach. Throughout his life, in Scotland, Cuba, and Florida, Sturrock saw lands denuded of trees needed for timber, windbreaks, or shade. His experience in Soledad gave him knowledge of the species with the most rapid growth and the desirable shape or root system. His reports to his superiors at Harvard are dominated by pages of notes, observations, and recommendations on timber trees at Soledad that were never included in published annual reports. He was deeply shocked by the report that his growth study plantations at Soledad and his timber plantings elsewhere in Cuba had been cut quickly and completely for charcoal in the early stages of the Castro administration.

Late in his life, David Sturrock turned to wood carving for relaxation. He experimented with a variety of tropical woods to achieve the minute detail he sought, at first carving scenes from Cuba which his wife sketched in outline. His work was accepted artistically and scientifically, and fifteen carved panels, representing Florida trees and Seminole Indians, are displayed in the public library of West Palm Beach. Thirteen panels, representing the vegetation of different geologic periods, and a twenty-foot panel on the evolution of man, are in the Science Museum and Planetarium of Palm Beach County.

David Sturrock preferred to be called a "plantsman" for his broad interest in all plants and their environment. He indeed had a comprehensive knowledge and many talents. To the student he was patient, understanding, and willing to share any knowledge he had. To me he was mentor and friend. He died July 8, 1978, and was buried in Hillcrest Memorial Park in West Palm Beach, Florida. He is survived by his wife, Ruth Esther Earle Sturrock, and four children, of whom he was justly proud: James P. Sturrock, an aerospace engineer; Thomas T. Sturrock, a professor of botany and administrator; Ruth Mary Sturrock, an electron microscopist; and Peter E. Sturrock, a professor of chemistry.

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LEAF ANATOMY AND VENATION PATTERNS OF THE STYRACACEAE[1]

WILLIAM E. SCHADEL AND WILLIAM C. DICKISON

THE STYRACACEAE is a woody, dicotyledonous family that is generally described as containing 12 or 13 genera and 150 to 190 species (Wood & Channell, 1960; Hutchinson, 1973; Gonsoulin, 1974; Spongberg, 1976). The plants are distributed primarily in eastern Asia to western Malaysia, tropical South America, and the southeastern United States. Ecologically, the plants occupy a variety of habitats.

The largest genus, *Styrax* L., includes about 120 species and is widely distributed in the tropical and warm temperate regions of eastern Asia and America. A conspicuous exception to this distribution pattern is *Styrax officinalis* L., which is found in the Mediterranean region and in California. In Asia the numerous species extend from the eastern Himalayas to Malaysia, Indochina, Korea, and Japan. The New World species are widely distributed from Pacific to Atlantic North America, the West Indies, southward to Venezuela and southern Brazil.

Two sections of the genus were recognized by Perkins (1907): STYRAX (*Eustyrax* Perk.), with the ovary 16- to 24-ovulate, and FOVEOLARIA (Ruiz & Pavon) Perk., with the ovary 3- to 5-ovulate. Section STYRAX was divided by Gürke (1891) and Perkins (1907) into two series, Valvatae and Imbricatae, on the basis of aestivation of the corolla lobes. As van Steenis (1932) has shown, however, imbrication varies widely with respect to both individual plants and species. The genus *Halesia* Ellis ex Linnaeus (about 5 species) occurs in southeastern North America and in eastern Asia, *Bruinsmia* Boerlage & Koorders (2 species) is found in Assam, Burma, and Malaysia (excluding the Malay Peninsula), *Pamphilia* Martius ex A. de Candolle (3 species) is located in Brazil, and *Afrostyrax* Perkins & Gilg (2 species), which according to Baas (1972) is better placed in the family Huaceae of the Malvales, occurs in tropical Africa. The remainder of the genera are distributed from the Himalayas through China and Japan: *Alniphyllum* Matsumura (8 species), China and Formosa; *Pterostyrax* Siebold & Zuccarini (7 species), Burma to Japan; *Rehderodendron* Hu (10 species), China and Indochina; *Huodendron* Rehder (6 species), southern China, Siam, and Indochina; *Sinojackia* Hu (3 species), southern China; *Parastyrax* W. W. Smith (1 species), Burma; and *Melliodendron* Handel-Mazzetti (3 species), southern and southwestern China.

As reviewed by Spongberg (1976), the flowers of the Styracaceae are

[1] This study represents a portion of a thesis submitted by W. E. Schadel to the Graduate School, The University of North Carolina at Chapel Hill, in partial fulfillment of the requirements for the Master of Arts degree.

perfect and actinomorphic. Inflorescences are often reduced, and the flowers are usually arranged in simple or sometimes branched, terminal and/or axillary racemes, corymbs, or panicles and are sometimes solitary or in few-flowered fascicles. The calyx is often articulated at the base, synsepalous, tubular, subentire or 4- or 5-lobed (rarely more), often united into a tube only at the base. The insertion of the corolla is hypogynous to epigynous, and the lobes are valvate or imbricate in bud. The stamens are usually twice the number of the corolla lobes, sometimes more; epipetalous; inserted in 1 whorl on the base of the corolla (or rarely at the base of the ovary), with the filaments usually being connate into a tube below (free above) and the anthers being 4-locular. The gynoecium is syncarpous. The ovary is superior and completely free to inferior and completely adnate to the calyx tube and is 3- to 5-locular, often 1-locular above. Each locule has 1 to many ovules on axile placentae. Each flower has a single slender style terminated by a usually 3- to 5-lobed stigma. The fruits are dry, often woody, dehiscent or indehiscent capsules or drupes, and the seeds number from 1 to many. The embryo is usually straight with broad cotyledons and is embedded in a fleshy endosperm.

In the general systems of Bentham and Hooker (1876), Engler and Prantl (Perkins, 1907), Bessey (1915), Cronquist (1968), Thorne (1968, 1976), and Takhtajan (1969, 1973), there is general agreement on the placement of the Styracaceae in the Ebenales. This same treatment was followed by G. Wagenitz (1964) in the latest edition of Engler's *Syllabus der Pflanzenfamilien*. Hutchinson (1926, 1959, 1967, 1969, 1973), however, placed the family in the order Styracales, along with the families Lissocarpaceae and Symplocaceae. The families Ebenaceae, Sapotaceae, and Sarcospermataceae were considered to constitute the distinct order Ebenales. Hutchinson (*op. cit.*) derived the Styracales from the Rosales via the Cunoniales and derived the Ebenales (*sensu stricto*) from the Myrsinales. Huber (1963) suggested a relationship between Symplocaceae and Styracaceae and the Cornaceae, incorporating them in the order Cornales which he derived from the Cistiflorae, especially Theaceae. Airy Shaw (in Willis, 1973) denied affinities between Symplocaceae and Styracaceae. According to Airy Shaw (*op. cit.*), Styracaceae is related to Philadelphaceae (also placed in the Cornales by Huber), and Symplocaceae is related to Theaceae. Cronquist (1968), Thorne (1968, 1976), and Takhtajan (1969, 1973) were of the opinion that the Ebenales, including the families Sapotaceae, Ebenaceae, Symplocaceae, Styracaceae, and Lissocarpaceae, form a natural group and that the origin of the order lies among the thealean complex. According to Wood and Channell (1960), these 5 families are characterized by sympetalous corollas with stamens generally two to three times as many as the corolla lobes (or, by abortion, equal in number to and opposite them) and by superior to inferior, incompletely to completely loculed ovaries with axile placentation. Wagenitz (1964) concluded that the Ebenales should also include two additional families, Hoplestigmataceae and Sarcospermataceae. Dahlgren (1975) felt that only the families Styracaceae, Sapotaceae, Lissocarpaceae, and Ebenaceae comprised the

Ebenales and that the Symplocaceae was better placed in Theales. According to Nooteboom (1975), Symplocaceae does not belong in the Ebenales but shows more affinity to Cornaceae and possibly Theaceae on the basis of evidence derived from chromosome numbers, chemotaxonomy, anatomy (wood and leaf), germination studies, and a survey of morphological characters. Such arguments indicate that the order Ebenales (*sensu lato*), including the families Lissocarpaceae, Styracaceae, Ebenaceae, Sapotaceae, and Symplocaceae, may not be a very natural assemblage and is in need of redefinition.

The first comprehensive anatomical investigation of styracaceous leaves was the family treatment by Solereder (1908). Metcalfe and Chalk (1950) provided additional observations, but information regarding the leaf anatomy of this family is still very incomplete. Other literature containing general information about leaf characters includes work by Gürke (1891), Perkins (1907, 1928), Mori (1936), Mears (1972), Baas (1972), Fahn (1974), Gonsoulin (1974), Hickey and Wolfe (1975), and Sarcar and Banerji (1975).

The present research was undertaken to examine the leaf anatomy (including venation patterns) of the Styracaceae in order to provide additional evidence for generic circumscription and to shed additional light on the intrafamilial and interfamilial relationships of the family. The specific objectives of this initial investigation are: 1) to provide a comprehensive description of the leaf structure of the Styracaceae, 2) to outline basic trends of structural specialization in the anatomy and architecture of styracaceous leaves, and 3) to provide anatomical data that will eventually contribute to a better understanding of the intrafamilial and interfamilial systematics and relationships of the family.

MATERIALS AND METHODS

Leaves from all 12 genera recognized as comprising the family Styracaceae (*sensu* Hutchinson, 1973) were studied. Material of the related genus *Lissocarpa* (Lissocarpaceae, 2 species, tropical South America) was also examined. A total of 82 species were investigated (APPENDIX). Transverse sections of leaves were prepared according to standard procedures of paraffin embedding and sectioning (Johansen, 1940). Sections were taken from the central part of the lamina (including the midrib) and from the basal, medial, and distal portions of the petiole. Since almost all specimens were gathered from dried herbarium collections, it was necessary to reexpand the leaves initially in 5 percent NaOH before fixation in 70 percent FAA and dehydration. Transverse sections were stained with safranin and fast-green. Cleared leaves were prepared using the NaOH method outlined by Arnott (1959) and were subsequently stained with safranin. Using cleared leaves and temporary free-hand peels, stomatal patterns were observed. Ten stomata per specimen were measured at the widest part of the guard cell pair and from pole to pole. Averages and ranges for stomatal width and length were recorded. Drawings were made

using a Wild dissecting microscope with a drawing tube attachment. Photomicrographs of transverse sections and cleared preparations were made using a Zeiss photomicroscope.

For the description of leaf architecture, the terminology of Hickey (1973), with necessary additions and modifications, was followed. For the genus *Styrax* the masculine gender was implemented following the suggestion of Nicolson and Steyskal (1976).

Slides are deposited in the Department of Botany, The University of North Carolina at Chapel Hill, and in the Department of Botany, Smithsonian Institution, Washington, D. C.

OBSERVATIONS

Summary of Leaf Anatomy of the Styracaceae (*sensu stricto*)

Petiole transverse section. Cuticle smooth or minutely furrowed. Epidermis uniseriate. Epidermal cells irregular to more or less rectangular to square in outline and with moderately thin walls. Parenchymatous cortex undifferentiated except in the monotypic genus *Parastyrax*, where outer half is collenchymatous and inner half parenchymatous. Crystals occurring as scattered druses, scattered prismatic crystals, a combination of druse and prismatic crystals, or, as in *Parastyrax*, crystal sand. Numerous solitary and clustered brachysclereids present in *Huodendron*.

Vasculature of petiole variable within the family. Five different vascular configurations occurring in basal portion of petiole: 1) arc, 2) arc with two dorsal cortical bundles, 3) arc with invaginated ends, 4) arc with invaginated ends and two dorsal collateral bundles, and 5) dissected cylinder of collateral bundles with numerous medullary bundles and four smaller dorsal dissected cylinders. At distal end of petiole, the following patterns occur:

1) Arc with invaginated ends: *Styrax americanus* var. *americanus* (Plate III, C), *S. americanus* var. *pulverulentus*, *S. hypargyreus*, *S. parallеloneurus*.

2) Arc with invaginated ends accompanied by two dorsal cortical bundles: *Pamphilia aurea* (Plate III, A), *P. pedicellata* var. *ovalis*, *P. styracifolia*, *Styrax argenteus* var. *argenteus*, *S. argenteus* var. *lintonii*, *S. argenteus* var. *ramirezii*, *S. benzoin* (Plate IV, A), *S. camporum*, *S. formosanus*, *S. glaber*, *S. glabrescens* var. *glabrescens*, *S. glabrescens* var. *pilosus*, *S. grandifolius*, *S. henryi*, *S. hypoglaucus*, *S. japonicus* (Plate III, D), *S. langkongensis*, *S. obtusifolius*, *S. officinalis* var. *fulvescens*, *S. officinalis* var. *redivivus*, *S. philadelphoides*, *S. platanifolius*, *S. portoricensis*, *S. subcrenatus*, *S. suberifolius*, *S. sumatranus*.

3) Medullated cylinder: *Halesia macgregorii*, *Huodendron biaristatum*, *H. chunianum*, *H. tibeticum*, *Sinojackia henryi*, *S. rehderiana*, *S. xylocarpa* (Plate III, B), *Styrax agrestis*, *S. faberi*.

4) Medullated cylinder accompanied by two dorsal cortical bundles: *Alniphyllum eberhardtii*, *A. fortunei*, *A. hainanense*, *A. pterospermum*, *Halesia carolina*, *H. diptera* var. *diptera*, *H. diptera* var. *magniflora*, *Melliodendron wangianum*, *M. xylocarpum*, *Pterostyrax cavaleriei*, *P. corymbosus*, *P. hispidus*, *Rehderodendron indochinense*, *R. kweichowense* (PLATE II, B), *R. macrocarpum*, *Styrax ochraceus* (PLATE IV, C), *S. serrulatus*.

5) Medullated cylinder accompanied by medullary vascular tissue and two dorsal cortical bundles: *Bruinsmia styracoides*, *Styrax ambiguus*, *S. cespedesii*, *S. conterminus*, *S. crotonoides*, *S. davillifolius*, *S. fanshawei*, *S. ferrugineus*, *S. glabratus*, *S. heteroclitus*, *S. jaliscanus*, *S. latifolius*, *S. longifolius*, *S. macrocalyx*, *S. macrotrichus*, *S. martii*, *S. micrasterus* (PLATE IV, B), *S. microphyllus*, *S. ovatus*, *S. pallidus*, *S. pearcei*, *S. pentlandianus*, *S. pohlii* (PLATE IV, D), *S. poissonianus*, *S. pseudargyrophyllus*, *S. subcordatus*, *S. yapobodensis*.

6) Dissected cylinder of collateral bundles with numerous medullary bundles and two smaller dorsal dissected cylinders: *Parastyrax lacei* (PLATE II, A).

All cortical bundles in the family collateral except in *Styrax argenteus*, *S. davillifolius*, and *S. pohlii* (PLATE IV, D), where amphicribral bundles occur. Perivascular sclerenchymatous elements present distally. As vascular tissue enters lamina, configuration remains same as in distal portion of petiole for all species investigated except *Pamphilia* (PLATE III, A) and *Parastyrax* (PLATE II, A).

Petiole and lamina surface view. Trichomes present in all species investigated except *Halesia macgregorii*. They generally occur on petiole, as well as on both surfaces of lamina, in four combinations of structural types: 1) stellate only, 2) peltate only, 3) stellate and peltate, and 4) stellate and simple cylindrical. Cuticle smooth or striated. Within individual cells striations oriented in a single direction parallel to one another and sometimes continuous from cell to cell. Laminar epidermal cells of both surfaces varying in shape from irregular to more or less quadrangular to polygonal. Epidermal anticlinal cell walls moderately thin except in *Styrax argenteus*, *S. camporum*, *S. heteroclitus*, and *S. macrotrichus*, where moderately thick walls occur. Anticlinal cell walls of adaxial epidermis generally straight to slightly curved, being slightly sinuous to curved only in *Huodendron biaristatum*, *H. chunianum*, *Styrax glabrescens*, and *S. serrulatus*. Anticlinal cell walls of abaxial epidermis straight to slightly curved, slightly sinuous to curved, or sinuous. For all species investigated, stomata anomocytic, occurring only on abaxial surface, and ranging in mean width between 11 and 22 μm. and in mean length between 14 and 30 μm.

Venation pinnate, with the single midvein following a straight, unbranched course. Midvein of moderate size (1.25–2.00 percent) except

in *Sinojackia* (PLATE VI, E) and *Styrax platanifolius*, where it is thin (less than 1.25 percent). Midvein ensheathed by sclerenchymatous elements elongate along long axis. In *Parastyrax* (PLATE VI, B) venation actinodromous with a pair of lateral primary veins occurring on either side of a third, centrally located primary vein. The imperfectly developed, reticulate actinodromous lateral veins becoming attenuate exmedially and with secondary veins originating exmedially. In all pinnately veined species, secondary venation weakly cladodromous, eucamptodromous, or transitional from eucamptodromous basally to brochidodromous distally. In species that are brochidodromous distally, loop-forming branches of secondaries join superjacent secondaries at right and acute angles. Relative thickness of secondary veins moderate, and their course branched when cladodromous, uniformly curved when eucamptodromous, and abruptly curved when brochidodromous. Exmedially, they are attenuate except for brochidodromous veins, which are of uniform thickness, and are braced in all species by a system of tertiary and quaternary veins. Simple intersecondary veins occurring in all species investigated except *Halesia macgregorii* (PLATE V, G), *Rehderodendron* (PLATE VI, D), *Sinojackia* (PLATE VI, E), *Styrax conterminus*, *S. martii*, *S. officinalis* (PLATE VI, I), *S. subcordatus*, *S. subcrenatus*, *S. suberifolius*, and *S. yapobodensis*, in which intersecondary veins are composite. Intramarginal veins absent in all species. Tertiary veins originating from secondary veins at acute, right, and obtuse angles, their pattern varying within the family from percurrent to random reticulate. Percurrent tertiary veins simple to forked and close in all species in which they occur, except in the specimen of *Parastyrax* examined, where they are both closely and distantly arranged. Predominantly opposite percurrent tertiary veins have a constant oblique tertiary angle in *Parastyrax*, *Styrax argenteus* (PLATE VI, G), and *Styrax benzoin*, and an apically decreasing oblique tertiary angle in *Alniphyllum eberhardtii* (PLATE V, C), *Pterostyrax* (PLATE VI, C), and *Styrax jaliscanus*. Predominantly alternate percurrent tertiary veins have a constant oblique tertiary angle with the midvein in *Styrax cespedesii* and *Styrax macrotrichus*, and an apically decreasing oblique tertiary angle in *Alniphyllum fortunei*, *A. hainanense*, *A. pterospermum* (PLATE V, D), *Styrax crotonoides*, *S. heteroclitus*, and *S. latifolius*. In other species, tertiary veins percurrent only in basal portion of leaf and forming random reticulate patterns distally. Predominantly opposite percurrent tertiary veins occurring only in a basal position in *Huodendron chunianum*, *Styrax conterminus*, *S. ovatus*, *S. paralleloneurus*, and *S. yapobodensis*; predominantly alternate percurrent tertiary veins, only in a basal position in *Melliodendron* (PLATE V, I), *S. ambiguus*, *S. ferrugineus*, *S. glabrescens*, *S. henryi*, *S. hypoglaucus*, *S. langkongensis*, *S. longifolius*, *S. macrocalyx*, *S. martii*, *S. pentlandianus*, *S. poissonianus*, *S. pseudargyrophyllus*, *S. serrulatus*, *S. subcordatus*, *S. suberifolius*, and *S. sumatranus*. In all other cases, tertiaries form random reticulate patterns throughout leaf. Resolution of higher vein orders distinct. Quaternary and quinary veins follow a relatively random course, having bundle sheaths of either parenchymatous or

sclerenchymatous elements elongate along their long axes. Bundle sheaths predominantly sclerenchymatous, with parenchymatous sheathing occurring only in *Alniphyllum*, *Bruinsmia*, *Parastyrax*, *Styrax americanus*, *S. argenteus*, and *S. platanifolius*. Ultimate veinlets simple to branched, linear to curved, generally with weak bundle sheaths composed of elements similar to sheathing of their respective higher vein orders. Sheathing absent on ultimate veinlets in *Alniphyllum*, *Bruinsmia*, *Halesia* (except *H. macgregorii*, where present), *Melliodendron*, *Parastyrax*, and *Pterostyrax*. Marginal ultimate venation either incomplete or looped. Areoles irregular to quadrangular to polygonal in shape (PLATE VII, A–F). They are small (less than 0.3 mm.) in *Styrax crotonoides*, *S. pseudargyrophyllus*, and *S. suberifolius*; small and medium (0.3–1.0 mm.) in *Parastyrax*, *Styrax paralleloneurus*, and *S. sumatranus*; large (1.0–2.0 mm.) in *Styrax japonicus*; both medium and large in *Bruinsmia*; and medium in all other species investigated. Areolation imperfectly or well developed, being incomplete only in the specimens of *Styrax japonicus* examined. Areoles relatively randomly arranged except in *Huodendron biaristatum*, *H. chunianum*, *Sinojackia*, *Styrax crotonoides*, *S. pseudargyrophyllus*, *S. subcrenatus*, and *S. suberifolius*, where well developed and relatively highly oriented.

Minute, crenulate teeth present in some species investigated are vascularized by a tertiary vein that is slightly expanded at base of tooth and tapered near apex (PLATE VIII, A–D). A glandlike cap composed of thin-walled cells occurring at apex of each tooth. Such glandlike structures also occurring on the entire margins of *Styrax glabrescens*. Scattered circular glands, consisting of five to eight small, flattened cells surrounding a centrally depressed area, occurring on lower leaf surface of a few species of *Styrax*.

Lamina transverse section. Cuticle thicker on adaxial surface than on abaxial in about half of species investigated, and of equal thickness on both surfaces for other species. For all species adaxial cuticular thickness ranging from less than 1 μm. to 24 μm.; abaxial cuticular thickness, from less than 1 μm. to 4 μm. Epidermal cells of both surfaces thin-walled and irregular to more or less rectangular to square. Epidermis uniseriate except in *Styrax macrotrichus* (PLATE X, A), *S. micrasterus* (PLATE X, B), *S. portoricensis* (PLATE X, E), and *S. pseudargyrophyllus* (PLATE X, F), where biseriate epidermis (hypodermis?) is present. Abaxial epidermal cells smaller than adaxial cells. Anomocytic stomata level with or slightly raised above abaxial surface. All major veins raised above abaxial leaf surface.

Bifacial mesophyll composed of 1 or 2 layers of slightly to very elongate palisade parenchyma cells in all species except *Styrax ochraceus* (PLATE X, C), which has 2 or 3 distinct layers of palisade cells, and *Styrax macrotrichus* (PLATE X, A), *S. poissonianus*, and *S. portoricensis* (PLATE X, E), with only a weakly differentiated mesophyll of irregular to more or less rectangular parenchyma cells. Spongy tissue very compact, moderately

compact, or loose, generally consisting of more or less isodiametric to slightly lobed parenchyma cells. Secondary and tertiary veins with sclerenchymatous bundle sheaths composed of elements elongate along their long axes. Bundle sheath extensions present in some species, occurring in two patterns of positions, adaxial only, and adaxial and abaxial. They are composed of sclerenchymatous elements elongate along long axis of veins. In *Pamphilia aurea* Martius (PLATE IX, D) (*Irwin et al. 20974* and *29208*) some elements of bundle sheath extensions also elongate perpendicular to long axis of veins. Quaternary and quinary veins with predominantly sclerenchymatous sheaths (occurring only in *Alniphyllum*, *Bruinsmia, Parastyrax*, *Styrax americanus*, *S. argenteus*, and *S. platanifolius*) and generally lacking bundle sheath extensions. Crystals present in all plants investigated, occurring as scattered druses, scattered prismatic crystals, a combination of druse and prismatic crystals, or, as in *Parastyrax*, crystal sand. They are sometimes confined to cortical parenchyma of midrib and to parenchyma cells adjacent to veins. Vasculature of midrib variable within the family, consisting of an arc, usually with invaginated ends, a medullated cylinder, or a medullated cylinder with medullary vascular tissue. Midrib with perivascular sclerenchymatous elements in all species investigated except *Styrax americanus*. In *Parastyrax* the central actinodromous vein has a ring of collateral bundles surrounding a single collateral bundle. All collateral bundles have thin-walled sclerenchymatous caps.

Lissocarpa Bentham
(Lissocarpaceae, *sensu* Engler & Gilg, 1924)

Petiole transverse section. Cuticle smooth, epidermis uniseriate. Epidermal cells irregular in outline and with moderately thick walls. Parenchymatous cortex undifferentiated, containing prismatic crystals and numerous diffuse vesiculose sclereids (*sensu* Rao & Bhupal, 1973) irregular in outline. Basally, vascular tissue consists of an arc with invaginated ends accompanied by two dorsal collateral bundles (PLATE I, B). Medially, each invaginated end of the arc begins to fold back upon itself dorsally. Distally, dorsal folding of each invaginated end of the arc increases. Perivascular sclerenchymatous elements present both singly and in clusters. As vascular tissue of petiole enters lamina, products of dorsal folding separate from arc and subsequently fuse, forming a dorsal plate. Ends of arc also fuse, forming a medullated vascular cylinder.

Petiole and lamina surface view. Surface of petiole and lamina glabrous. Cuticle smooth. Adaxial epidermal cells of lamina irregularly shaped with moderately thick, extremely sinuous anticlinal walls. Abaxial epidermal cells resembling cells of upper surface. Diffuse vesiculose sclereids with numerous simple pits occurring singly and in clusters throughout mesophyll and in random association with vascular tissue. For the genus, stomata anomocytic, occurring only on abaxial surface, ranging in mean width between 28 and 29 μm., and in mean length between 34 and 38 μm.

Venation pinnate, with single midvein following a straight, unbranched course. Midvein of moderate size (1.25–2.00 percent) and ensheathed by thick-walled sclerenchymatous elements. Secondary venation weakly brochidodromous and ensheathed by thick-walled sclerenchymatous elements elongate along long axis of veins. Acute angle of divergence, nearly uniform for all secondaries, is wide. Secondary veins relatively slender, their course abruptly curved; loop-forming branches of secondaries joining superjacent secondaries at right and acute angles and braced exmedially by system of tertiary and quaternary veins. Composite intersecondary veins present, but intramarginal veins absent. Tertiary veins originate from secondaries at acute, right, and obtuse angles, forming random reticulate pattern. They are ensheathed by moderately thick-walled sclerenchymatous elements elongate along long axis of veins. Resolution of higher vein orders not distinct. They consist of a ramified network terminating in numerous branched ultimate veinlets. Higher vein orders and ultimate veinlets ensheathed by thin-walled, irregular to rectangular sclerenchymatous elements elongate along their long axes. Marginal ultimate venation fimbriate. Imperfectly developed, randomly arranged areoles irregularly shaped and large (1.0–2.0 mm.). Teeth and glands absent.

Lamina transverse section. Cuticle thicker adaxially (5–6 μm.) than abaxially (3–4 μm.). Epidermis uniseriate. Epidermal cells of adaxial surface thin-walled and irregular to more or less rectangular in outline; those of both surfaces approximately equal in size. Anomocytic stomata level with abaxial leaf surface. All major veins raised above abaxial leaf surface.

Bifacial mesophyll with 1 or 2 layers of short, more or less rectangular palisade parenchyma cells and several layers of fairly loose spongy tissue of isodiametric to slightly lobed cells. Sclerenchymatous bundle sheaths without bundle sheath extensions are conspicuous around all orders of venation. Prismatic crystals confined to parenchyma cells adjacent to veins. Diffuse vesiculose sclereids, irregularly shaped in outline, occurring in mesophyll. Midrib with medullated vascular cylinder accompanied by dorsal plate. Perivascular sclerenchymatous elements present.

Afrostyrax Perkins & Gilg

Petiole transverse section. Cuticle smooth, epidermis uniseriate. Epidermal cells square to rectangular in outline and with moderately thin walls. Parenchymatous cortex undifferentiated except in one specimen of *Afrostyrax kamerunensis* (*Mildbraed 10688* (A)), where small amount of periderm and 2 or 3 layers of collenchyma observed in outer portion of cortex. Cortex containing prismatic crystals. Basally and medially, vascular tissue of petiole consisting of two large, C-shaped vascular bundles and one smaller, abaxially positioned one (PLATE I, A). Distally, the two large, C-shaped lateral bundles invaginate at the dorsal ends. Perivascular sclerenchymatous elements present. As vascular tissue of petiole

enters lamina, invaginated dorsal ends of C-shaped lateral bundles separate from lateral bundles, subsequently becoming medullary bundles. The two lateral C-shaped bundles fuse dorsally, enclosing the medullary bundles, which vary in number from one to several depending on whether invaginated portions fuse or divide. Baas (1972) reports *A. lepidophyllus* as having a more complex vascularization than *A. kamerunensis* as the result of a larger, although variable, number of medullary bundles present.

Petiole and lamina surface view. Stellate trichomes occurring infrequently on petiole and lamina of both species. Numerous peltate scales and short, uniseriate, two- to three-cellular trichomes occurring on petiole and lamina surfaces of *Afrostyrax lepidophyllus* but lacking on *A. kamerunensis*. Cuticle smooth. *Afrostyrax lepidophyllus* with adaxial epidermal cells of lamina quadrangular to polygonal, and having thin, slightly sinuous to curved anticlinal walls; *A. kamerunensis*, however, with anticlinal epidermal walls very sinuous. With exception of cells underlying major veins and resembling cells of adaxial surface, abaxial epidermis of *A. lepidophyllus* almost completely composed of dome-shaped papillate cells. This condition absent in *A. kamerunensis*, where abaxial epidermal cells smaller but otherwise identical to upper surface cells (which have very sinuous anticlinal walls). For the genus, stomata paracytic with crescent-shaped subsidiary cells, occurring only on abaxial surface. Mean stomatal width 11 μm.; mean length ranging between 15 and 16 μm.

Venation pinnate, with single midvein following a straight, unbranched course (PLATE V, A). Midvein of moderate size (1.25–2.00 percent) ensheathed by moderately thick-walled sclerenchymatous elements elongate along long axis of midvein. Secondary venation transitional from eucamptodromous basally to brochidodromous distally, also ensheathed by moderately thick-walled sclerenchymatous elements elongate along long axis of veins. Acute angle of divergence, nearly uniform for all secondaries, moderate. Relative thickness of the secondary veins moderate, their course uniformly curved. Exmedially, secondary veins are attenuate and braced by system of tertiary and quaternary veins. Intersecondary and intramarginal veins absent. Tertiary veins originating from secondaries at approximately right angles and forming orthogonal reticulate patterns with other tertiaries. They have a sheath of thin-walled parenchymatous cells slightly elongate along long axis of veins. Resolution of higher vein orders distinct. Both quaternary and quinary veins following an orthogonal course and having weak, incomplete parenchymatous sheaths. The few ultimate veinlets simple, linear to curved, without sheathing. Marginal ultimate venation fimbriate. The well-developed, oriented areoles quadrangular and small (less than 0.3 mm.) (PLATE VII, A). Teeth absent, but oval-shaped glands composed of elongate, thin-walled cells present on lamina margins.

Lamina transverse section. Cuticle smooth and of equal thickness (less than 1 μm.) on both surfaces. Epidermis uniseriate. Epidermal cells of adaxial surface thin-walled and square to rectangular in outline.

Cells of abaxial surface smaller than adaxial cells. Majority of abaxial cells of *Afrostyrax lepidophyllus* papillate with an outer dome-shaped configuration (PLATE IX, A), a condition absent in *A. kamerunensis*. Paracytic stomata slightly raised above level of abaxial leaf surface. All major veins raised above level of abaxial leaf surface.

Bifacial mesophyll with 1 or 2 layers of elongate palisade parenchyma cells and two to several layers of moderately compact spongy tissue of more or less isodiametric to slightly lobed cells. Sclerenchymatous elements ensheathing secondary veins and forming adaxial and abaxial caps exterior to parenchymatous bundle sheaths of tertiaries. Both secondary and tertiary veins with conspicuous parenchymatous adaxial and abaxial bundle sheath extensions. Quaternary and quinary veins with weak, incomplete parenchymatous sheaths and parenchymatous adaxial and abaxial bundle sheath extensions. Prismatic crystals occurring in parenchyma cells adjacent to veins and in cortical region of midrib. Midrib with medullated vascular cylinder having variable number of medullary bundles. Perivascular sclerenchymatous elements present.

DISCUSSION AND CONCLUSIONS

Leaves of Styracaceae are considerably more variable morphologically and anatomically than previous descriptions indicate. Characters that are present in leaves of nearly all species investigated include bifacial mesophyll, anomocytic stomata confined to the abaxial surface, crystals in the form of druse and/or prismatic shapes, trichomes of the stellate, peltate, or simple cylindrical type, sheathing and supporting elements associated with the venation, and pinnate primary venation accompanied by camptodromous secondary venation.

Interestingly, almost all variation observed in the leaf structure of the ten smaller styracaceous genera is encountered among species of the large genus *Styrax*. Leaf characters that are not present in *Styrax* but which occur elsewhere in the Styracaceae include the distinct petiolar brachysclereids in *Huodendron*, the sclerenchymatous supporting sheath cells in *Pamphilia aurea* Martius (*Irwin et al. 20974* and *29208*) that are perpendicular to the long axis of the veins, and the unique features of crystal sand, actinodromous venation, and petiole vasculature in *Parastyrax*. Although many foliar characters appear to be extremely useful in the delimitation of taxa, a larger sample size is needed to confirm these observations.

Some of the anatomical variation lends itself to possible ecological interpretation, although the absence of detailed habitat data for many of the specimens observed makes such interpretation difficult. In coriaceous leaves, such as those of Brazilian *Pamphilia*, there does appear to be a strong correlation between more intensive sclerification along the veins and veinlets, the presence of inrolled leaf margins, thicker cuticles on both surfaces, compact spongy mesophyll, and an extremely dense indumentum on the abaxial surface of the leaves. Many of these characters have been

associated in other families with adaptations to a dry environment and may represent similar adaptation by styracaceous species. In leaves of species typically found in a mesic environment, such as *Halesia* (which occurs naturally in southeastern U. S. and China), there appears to be a strong correlation between less sclerification along the veins and veinlets, thinner cuticles on both surfaces, abundant air spaces in the spongy mesophyll, and less dense indumentum.

Relative levels of specialization of the foliar venation of woody dicots have been determined through comparative morphological studies of fossil and extant leaves (Hickey, 1971; Hickey & Doyle, 1972; Hickey, 1973; Hickey & Wolfe, 1975; Hickey & Doyle, 1977). Trends of specialization are represented by: 1) an increase in regularity of both low and high order venation; 2) a shift from indistinct vein orders to vein orders that are readily distinguishable from one another; 3) a shift from tertiary veins that follow a random course to tertiary veins that are very regular, often with rigid percurrent veins traversing the intercostal areas; and 4) a progressive development from random, incomplete areolation to orthogonal, well-developed (perfect) areolation. The venation of the Styracaceae is predominantly at an advanced level of organization in accordance with the above trends. The secondary veins are generally regular in course, and the tertiary veins linking the secondaries demonstrate trends toward being numerous, well differentiated, percurrent, and regularly spaced in a close arrangement. Another index of advancement is the formation of well-developed areoles of relatively constant size and placement in which veinlets are either absent or short and unbranched as in *Huodendron*, *Parastyrax*, *Sinojackia*, and several species of *Styrax*.

Petiole vasculature of the Styracaceae is quite diverse and, with the exception of that found in *Parastyrax*, consists of an arc, an arc with invaginated ends, a medullated cylinder, or a medullated cylinder with medullary tissue; these characters may or may not be accompanied by cortical bundles. In the leaves of several species of *Styrax*, the occurrence of both medullary and cortical petiolar vasculature is correlated with compact spongy mesophyll and an increase in leaf coriaceousness. Whereas each of the styracaceous genera except *Styrax* is characterized by a single vascular configuration, all observed patterns of petiole vasculature occur among species of the large genus *Styrax*. The presence in the petiole of *Parastyrax* of a highly dissected cylinder of collateral bundles that is accompanied by numerous medullary bundles and two smaller dorsal dissected cylinders is exceptional for the family.

Minute, crenulate teeth are present in all genera investigated except *Huodendron* and *Pamphilia*. Each tooth is vascularized by a medial vein that is usually slightly expanded at the base and tapered near the apex. A glandlike cap composed of thin-walled cells occurs at the apex of each tooth. Hickey and Wolfe (1975) described what they termed the "Theoid Tooth and its inferred variants" as present in the Ebenales, but it is not certain whether the typical styracaceous tooth morphology observed in this study falls within the limits of variation observed in that survey.

Although trichomes have traditionally been employed for systematic purposes in the Styracaceae (Perkins, 1907; Standley & Steyermark, 1940; Gonsoulin, 1974), it is clear that their morphological diversity has not yet been satisfactorily described. Among stellate trichomes, enormous variation within the family can be observed in such features as size, color, distribution, mode of attachment, appressed as opposed to stalked habit, number of arms, thickness of arms, degree of lateral fusion of arms, and number and orientation of cells composing each arm. Because of the large amount of gradation between these features, the value of stellate trichomes as diagnostic characters for separating taxa within the family is uncertain until these trichomes are more accurately characterized by employing a wider range of materials. The same difficulties are also evident, although to a much lesser extent, among peltate scales and simple cylindrical trichomes.

Baas (1972) presented evidence for the removal of *Afrostyrax* from the Styracaceae and for its subsequent placement in the malvalean family Huaceae. The present study affirms these conclusions. The number of characters separating the Huaceae from the Styracaceae is substantial. Characters distinguishing *Afrostyrax* leaves from styracaceous foliage include paracytic stomata, extremely well-developed, rectangular areolae, the presence of caducous stipules, and fimbriate marginal ultimate venation. According to Baas (1972), additional features distinguishing the Huaceae from the Styracaceae include the choripetalous corolla (vs. sympetalous in the Styracaceae), the 3-porate pollen (vs. 3-colporate), the trilacunar nodes (vs. unilacunar), and the cork arising in subepidermis (vs. in pericycle). The genus *Lissocarpa* was removed from the Styracaceae by Perkins (1907) and has subsequently been regarded as constituting the closely related monogeneric family Lissocarpaceae (*sensu* Engler & Gilg, 1924; Hutchinson, 1926, 1959, 1967, 1969, 1973). In addition to reproductive characters, features of foliar anatomy that can be used to separate *Lissocarpa* from the Styracaceae include diffuse vesiculose sclereids in the petiole and mesophyll, petiole vasculature consisting of an arc with outwardly curving ends, and fimbriate marginal ultimate venation.

The genus *Parastyrax* has a number of typical styracaceous floral characteristics (bisexual flowers axillary on new shoots; calyx subentire; petals 5, imbricate; stamens 10; anthers introrse; ovary usually inferior) but also has some leaf characters that are markedly different from the other styracaceous genera. These unique leaf characters include a distinctive petiolar vasculature, actinodromous primary venation, and the presence of crystal sand in the leaf mesophyll. Additional points of difference between *Parastyrax* and other taxa of the Styracaceae include its unusual height of 150 feet or more and its drupaceous fruit with a glabrous, fleshy exocarp marked with elongate, whitish lenticels (Smith, 1920). These distinguishing characters indicate that further intensive investigation of *Parastyrax* is warranted to discern more accurately its affinities with other styracaceous genera.

According to Wood and Channell (1960), the genus *Halesia* is most

closely related to *Pterostyrax*, *Rehderodendron*, *Sinojackia*, and *Melliodendron*. These five genera share a number of similar reproductive characters (including ovary two-thirds to completely inferior, four to eight ovules in each loculus, a single elongate style, and indehiscent fruit), as well as a substantial number of common leaf characters. According to Gonsoulin (1974), the genera *Alniphyllum* and *Pterostyrax* are most closely related to *Styrax*. *Alniphyllum* differs from *Styrax* mainly in its winged seeds and filaments connate distally to form a tube, whereas *Pterostyrax* differs from that genus primarily in its two-thirds to completely inferior ovary. These three genera share such reproductive characters as bisexual flowers, campanulate calyx, five corolla segments or free petals, ten stamens, and linear anthers. While it is true that there is a high correlation between the leaf characters of *Alniphyllum* and *Pterostyrax* and those of several species of *Styrax*, it is also true that almost all of the variation observed in the leaf characters of the ten small genera occurs in the large genus *Styrax*.

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APPENDIX. Specimens examined.

Afrostyrax kamerunensis Perk. & Gilg. Cameroons: *J. Mildbraed 10688* (A*); *G. Zenker 3922* (US). *A lepidophyllus* Mildbraed. Congo: *G. Gilbert 10222* (A), *J. Louis 3965* (US).

Alniphyllum eberhardtii Guillaumin. Indochina: *A. Petelot 4490* (US); *E. Poilane 19043* (A). *A. fortunei* Perk. Chimen, China: *R. C. Ching 3105* (A). *A. hainanense* Hay. Hainan, China: *C. I. Lei 442* (US). *A. pterospermum* Matsum. Formosa: *E. H. Wilson 9992* (US); label information illegible (US #1597269).

Bruinsmia styracoides Boerl. & Koord. New Guinea: *M. S. Clemens 2970* (A). North Borneo: *J. & M. S. Clemens 50339* (US).

Halesia carolina L. Jackson Co., North Carolina: *G. Nesom s.n.* (NCU). South Carolina: *H. D. House 1866* (US). *H. diptera* var. *diptera* Ellis. Jefferson Co.,

* Herbarium abbreviations follow Holmgren and Keuken (1974).

Mississippi: *W. B. McDougall 1430* (US). *H. diptera* Ellis var. *magniflora* Godfrey. Tallahassee, Florida: *R. K. Godfrey 71367* (US). *H. macgregorii* Chun. Chekiang, China: *Ching 2132* (US).

Huodendron biaristatum (W. W. Smith) Rehder. Indochina: *Petelot 6339* (US). *H. chunianum* Hu. Yunnan, China: *H. T. Tsai 60571* (A). *H. tibeticum* (Anthony) Rehder. Tibet: *J. F. Rock 22020* (US).

Lissocarpa benthamii Gürke. British Guiana: *H. A. Gleason 724* (GH). *L. guianensis* Gleason. British Guiana: *J. S. de la Cruz 3076* (GH); *N. Y. Sandwith 1590* (US).

Melliodendron wangianum Hu. Szechwan, China: *Chiao & Fan 364* (A). *M. xylocarpum* Handel-Mazz. Kwangsi-Chuang, China: *Ching 7132* (US). Kwangtung, China: *W. T. Tsang 26363* (A).

Pamphilia aurea Martius. Brazil: *H. S. Irwin, H. Maxwell, & D. C. Wasshausen 20974* (US); *Irwin et al. 29208* (GH). *P. pedicellata* var. *ovalis* Perk. Brazil: *Y. Mexia 5778* (US). *P. styracifolia* A. DC. Brazil: *J. E. de Oliveira s.n.* (US #2123954).

Parastyrax lacei W. W. Smith. Burma: *J. H. Lace s.n.* (E).

Pterostyrax cavaleriei Chun. Kweichow, China: *Y. Tsiang 6434* (US). *P. corymbosus* Sieb. & Zucc. Japan: *Y. Tateishi 7010* (US). *P. hispidus* Sieb. & Zucc. Königl. Botanischer Garten, Breslau, Poland: *C. Baenitz s.n.* (US #1155541).

Rehderodendron indochinense Li. Yunnan, China: *K. M. Feng 12307* (A). *R. kweichowense* Hu. Kwangsi, China: *S. K. Lau 28706* (A). *R. macrocarpum* Hu. Szechwan, China: *W. P. Feng 2663* (A); *T. C. Lee 2959* (US).

Sinojackia henryi (Dümmer) Merr. Szechwan, China: *A. Henry 8865* (GH). *S. rehderiana* Hu. Without location: *collector unknown 10314* (L). *S. xylocarpa* Hu. Kiangsu, China: *W. Cheng 4494* (US).

Styrax agrestis G. Don. Solomon Islands: *L. J. Brass 3261* (A). *S. ambiguus* Seub. Brazil: *E. Warming s.n.* (US #1110459). *S. americanus* var. *americanus* Lam. Florida: *F. Rugel s.n.* (US #512620). *S. americanus* Lam. var. *pulverulentus* (Michaux) Perk. Escambia Co., Alabama: *E. S. Ford 5242* (US). Hardin Co., Texas: *V. L. Cory 52817* (US). *S. argenteus* var. *argenteus* Presl. Nayarit, Mexico: *J. G. Ortega 60* (US). *S. argenteus* Presl var. *hintonii* (Bullock) Gonsoulin. Michoacán, Mexico: *Bro. G. Arsène 8472* (US). *S. argenteus* Presl var. *ramirezii* (Greenman) Gonsoulin. Chiapas, Mexico: *C. A. Purpus 157* (US). *S. benzoin* Dryander. Java, Indonesia: *Blume s.n.* (A). Trinidad, West Indies: *W. E. Broadway s.n.* (US #1194642). *S. camporum* Pohl. Brazil: *G. Hatschbach & O. Guimaraes 21776* (US); *L. O. Williams 6432* (GH). *S. cespedesii* Perk. Colombia: *E. L. Little, Jr. 8820* (US). *S. conterminus* Smith. El Salvador: *P. H. Allen 7184* (US). *S. crotonoides* Clarke. Singapore: *Field 36937* (A). *S. davillifolius* Perk. Venezuela: *A. Jahn s.n.* (US #1189096). *S. faberi* Perk. China: *C. O. Levine 467* (GH). *S. fanshawei* Sandwith. British Guiana: *D. B. Fanshawe 5607* (US). *S. ferrugineus* Nees & Martius. Brazil: *Irwin et al. 13659* (US); *G. O. A. Malme 1958a* (GH). *S. formosanus* Matsumura. Formosa: *Wilson 10266* (A). *S. glaber* Swartz. St. Kitts, West Indies: *R. K. Wadsworth 495* (A). *S. glabratus* Schott. Brazil: *A. Loefgren 4165* (US). *S. glabrescens* var. *glabrescens* Bentham. Mexico: *Purpus 88* (US). *S. glabrescens* Bentham var. *pilosus* Perk. Mexico: *E. Matuda 4179* (US). *S. grandifolius* Aiton. Garland Co., Arkansas: *C. F. Adams s.n.* (US #2420427). Gwinnett Co., Georgia: *H. A. Allard 194* (US). *S. henryi* Perk. Formosa: *Wilson 9933* (A). *S. heteroclitus* Macbride. Juanjui, Peru: *G. Klug 4282* (US). *S. hypargyreus* Perk. Venezuela: *H. Pittier 15725*

(US). *S. hypoglaucus* Perk. Kwangsi, China: *Tsang 24105* (A). *S. jaliscanus* S. Watson. Mexico: *C. A. Pringle 11012* (US). *S. japonicus* Sieb. & Zucc. Japan: *N. Fukuoka 5852* (US); *M. Hiroe 10251* (A). Washington, D. C.: *G. B. Sudworth s.n.* (US #478713). *S. langkongensis* W. W. Smith. Yunnan, China: *Rock 10546* (A). *S. latifolius* Pohl. Brazil: *collector unknown 7269* (US); *H. M. Curran 627* (GH). *S. longifolius* Standley. Peru: *R. Ferreyra 4546* (US). *S. macrocalyx* Perk. Colombia: *J. C. Mutis 2465* (US). *S. macrotrichus* Perk. Colombia: *Mutis 5207* (US). *S. martii* Seub. Brazil: *Irwin et al. 32264* (US). *S. micrasterus* Perk. Colombia: *Mutis 4260* (US). *S. microphyllus* Perk. Colombia: *Mutis 2558* (US). *S. obtusifolius* Griseb. Cuba: *R. A. Howard 5618* (US); *A. Gonzales 477* (A). *S. ochraceus* Urban. West Indies: *E. L. Ekman 13883* (US); *Bro. A. H. Liogier 11364* (GH). *S. officinalis* L. var. *fulvescens* (Eastw.) Munz & Johnston. California: *L. P. Abrams 6273* (US); *E. A. Purer 6680* (US). *S. officinalis* L. var. *redivivus* (Torrey) Howard. Placer Co., California: *E. Crum 2043* (US). *S. ovatus* A. DC. Peru: *Mexia 8171* (GH). *S. pallidus* A. DC. Venezuela: *L. Williams 10353* (A). *S. paralleloneurus* Perk. Sumatra, Indonesia: *H. O. Forbes 2354* (GH). *S. pearcei* Perk. Bolivia: *O. Buchtien 5953* (US). *Styrax pentlandianus* Remy. Bolivia: *A. Miguel 2867* (US). *S. philadelphoides* Perk. Chekiang, China: *H. H. Hu 1689* (A). Kiangsu, China: *L. F. Tsu s.n.* (US #1346056). *S. platanifolius* Engelmann. Kendall Co., Texas: *E. J. Parker 11474* (US). *S. pohlii* A. DC. Brazil: *collector unknown 2885* (US). *S. poissonianus* Perk. Peru: *C. Schunke A39* (US). *S. portoricensis* Krug & Urban. West Indies: *collector unknown s.n.* (US #404089). *S. pseudargyrophyllus* Sleumer. Colombia: *L. Muñoz s.n.* (US #1950764). *S. serrulatus* Roxb. Tibet: *G. H. Cave 1.9.1920* (A). *S. subcordatus* Moric. Brazil: *Irwin et al. 12490a* (GH). *S. subcrenatus* Handel-Mazz. Hainan, China: *F. C. How 71118* (A). *S. suberifolius* Hooker & Arnott. Kwangtung, China: *Tsang 25927* (A). Hong Kong: *W. Y. Chun 5071* (A). Taiwan: *A. Hsieh s.n.* (US #2063471). *S. sumatranus* J. J. Smith. Sumatra, Indonesia: *Yates 2532* (A). *S. yapobodensis* (Idrobo & R. E. Schultes) Steyerm. Colombia: *R. E. Schultes 14394* (A).

EXPLANATION OF PLATES

PLATE I

Transverse sections of petiole and midrib illustrating patterns of vascularization. A, *Afrostyrax kamerunensis* (*Zenker 3922*): 1, medial petiole; 2, distal petiole; 3, midrib 2 mm. from petiole; 4, midrib 4 mm. from petiole; 5, medial midrib. B, *Lissocarpa guianensis* (*de la Cruz 3076*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. Key to tissues: solid black, sclerenchyma; stipple, phloem; vertical lines, xylem.

PLATE II

Transverse sections of petiole and midrib illustrating patterns of vascularization. A, *Parastyrax lacei* (*Lace s.n.*): 1, medial petiole; 2, distal petiole; 3, midrib 5 mm. from petiole; 4, medial central actinodromous vein. B, *Rehderodendron kweichowense* (*Lau 28706*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. Key to tissues: solid black, sclerenchyma; stipple, phloem; vertical lines, xylem.

PLATE III

Transverse sections of petiole and midrib illustrating patterns of vascularization. A, *Pamphilia aurea* (*Irwin et al. 29208*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, midrib 2 mm. from petiole; 5, medial midrib. B, *Sinojackia xylocarpa* (*Cheng 4494*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. C, *Styrax americanus* (*Rugel s.n.*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. D, *Styrax japonicus* (*Fukuoka 5852*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. Key to tissues: solid black, sclerenchyma; stipple, phloem; vertical lines, xylem.

PLATE IV

Transverse sections of petiole and midrib illustrating patterns of vascularization. A, *Styrax benzoin* (*Broadway s.n.*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. B, *Styrax micrasterus* (*Mutis 4260*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. C, *Styrax ochraceus* (*Ekman 13883*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. D, *Styrax pohlii* (*collector unknown 2885*): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. Key to tissues: solid black, sclerenchyma; stipple, phloem; vertical lines, xylem.

PLATE V

Venation patterns (leaves not drawn to scale). A, *Afrostyrax kamerunensis* (*Zenker 3922*). B, *Lissocarpa benthamii* (*Gleason 724*). C, *Alniphyllum eberhardtii* (*Petelot 4490*). D, *Alniphyllum pterospermum* (*Wilson 9992*). E, *Bruinsmia styracoides* (*J. & M. S. Clemens 50339*). F, *Halesia carolina* (*Nesom s.n.*). G, *Halesia macgregorii* (*Ching 2132*). H, *Huodendron tibeticum* (*Rock 22020*). I, *Melliodendron xylocarpum* (*Ching 7132*).

PLATE VI

Venation patterns (leaves not drawn to scale). A, *Pamphilia aurea* (*Irwin et al. 20974*). B, *Parastyrax lacei* (*Lace s.n.*). C, *Pterostyrax hispidus* (*Baenitz s.n.*). D, *Rehderodendron indochinense* (*K. M. Feng 12307*). E, *Sinojackia xylocarpa* (*Cheng 4494*). F, *Styrax agrestis* (*Brass 3261*). G, *Styrax argenteus* var. *argenteus* (*Ortega 60*). H, *Styrax faberi* (*Levine 467*). I, *Styrax officinalis* var. *redivivus* (*Crum 2043*).

PLATE VII

Leaf areolation. A, *Afrostyrax kamerunensis* (*J. Mildbraed 10688*), × 107, well-developed areoles. B, *Huodendron biaristatum* (*Petelot 6339*), × 40, observe relatively consistent size and shape of areoles. C, *Sinojackia xylocarpa* (*Cheng 4494*), × 27, relatively well-developed areoles. D, *Styrax glabratus* (*Loefgren 4165*), × 36, imperfectly developed areoles. E, *Styrax japonicus* (*Fukuoka 5852*), × 27, incompletely developed areoles. F, *Styrax suberifolius* (*Chun 5071*), × 27, observe branching of ultimate veinlets and imperfectly developed areoles.

PLATE VIII

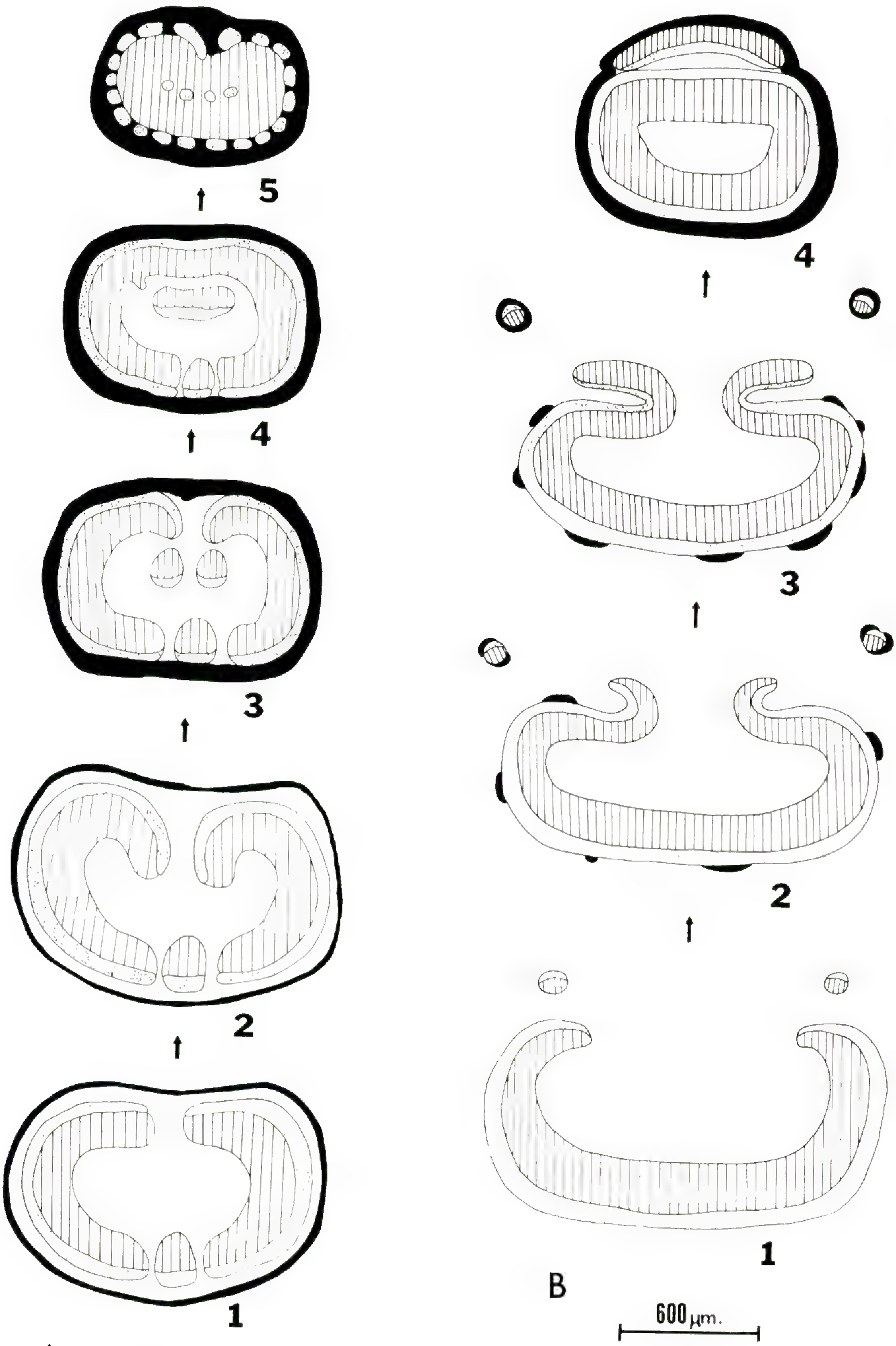
Tooth morphology. A, B, *Styrax serrulatus* (*Cave 1.9.1920*): A, × 40, note vascularization of tooth by tertiary vein. B, × 107, observe expansion of vascular tissue at base of tooth. C, *Styrax japonicus* (*Fukuoka 5852*), × 40, glandlike cap on apex of tooth. D, *Styrax faberi* (*Levine 467*), × 107, note tapering of vascular tissue at apex of tooth below glandlike cap.

PLATE IX

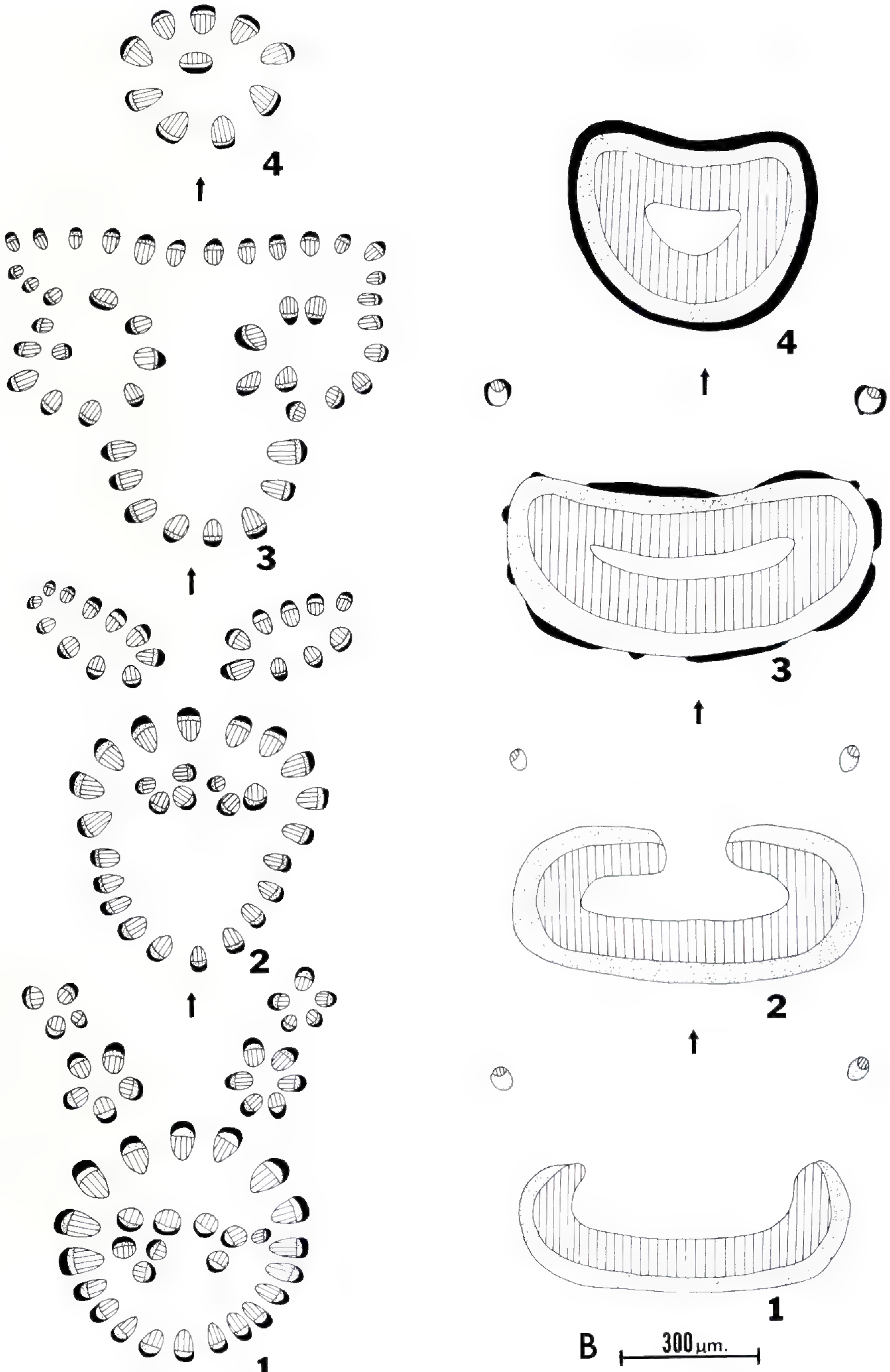
Transverse sections of lamina. A, *Afrostyrax lepidophyllus* (*Gilbert 10222*), × 400, note prominent papillate abaxial epidermis. B, *Bruinsmia styracoides* (*Clemens 2970*), × 160, observe isodiametric shape of spongy parenchyma cells. C, *Huodendron chunianum* (*Tsai 60571*), × 160, prominent cuticular striations on both surfaces. D, *Pamphilia aurea* (*Irwin et al. 29208*), × 107, note upright cells in adaxial sheath extension. E, *Styrax ferrugineus* (*Irwin et al. 13659*), × 160, observe prominent adaxial bundle sheath extension. F, *Styrax glaber* (*Wadsworth 495*), × 160, note absence of bundle sheath extension.

PLATE X

Transverse sections of lamina. A, *Styrax macrotrichus* (*Mutis 5207*), × 265, observe weakly differentiated mesophyll. B, *Styrax micrasterus* (*Mutis 4260*), × 160, note compact spongy parenchyma. C, *Styrax ochraceus* (*Ekman 13883*), × 135, observe three layers of palisade parenchyma. D, *Styrax philadelphoides* (*Tsu s.n.*), × 160, bundle sheath extensions occurring in both adaxial and abaxial positions. E, *Styrax portoricensis* (US #404089), × 265, observe weakly differentiated mesophyll. F, *Styrax pseudargyrophyllus* (*Muñoz s.n.*) × 160, note biseriate epidermis (hypodermis?).



SCHADEL & DICKISON, LEAF ANATOMY



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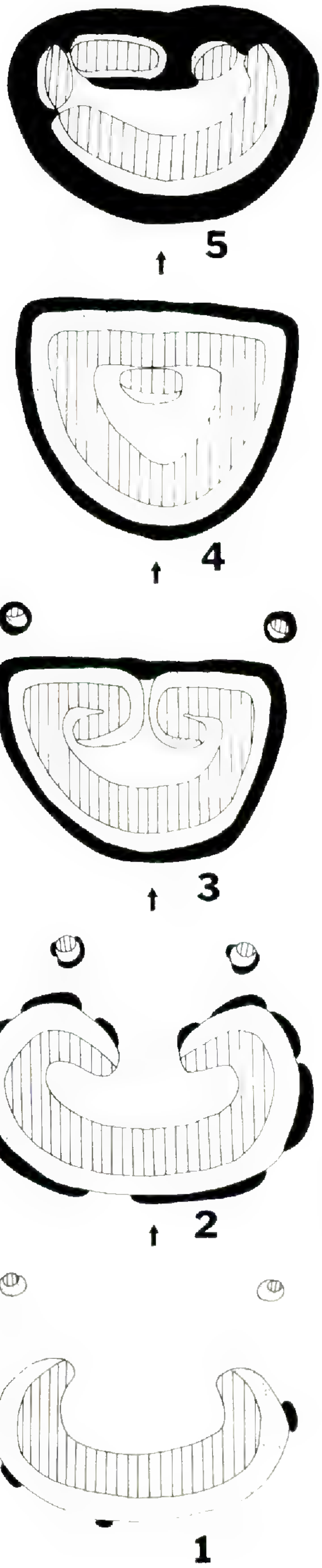

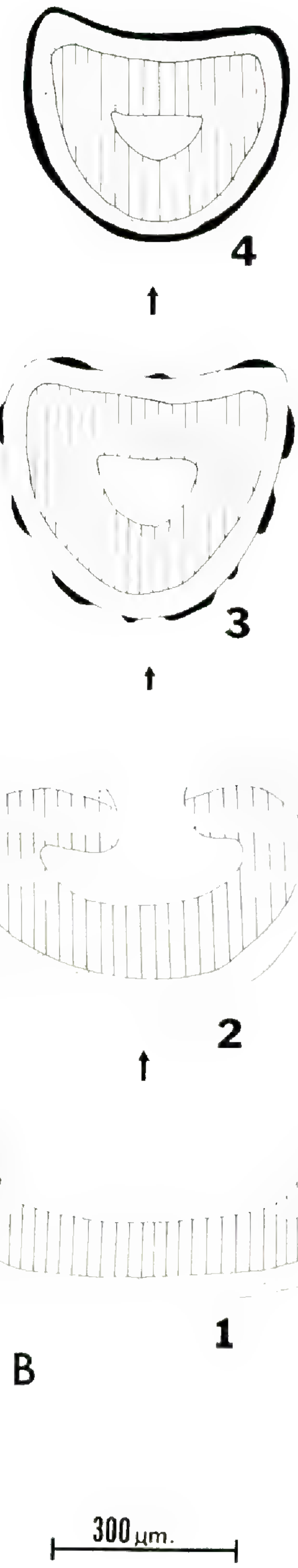

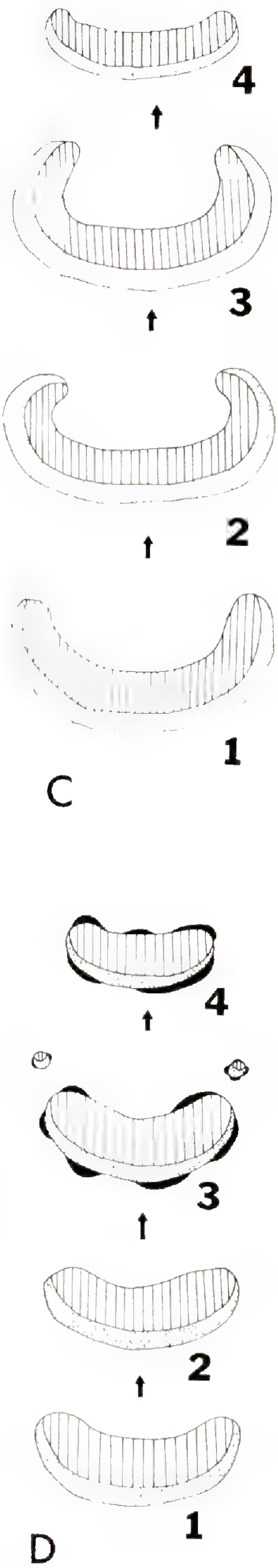

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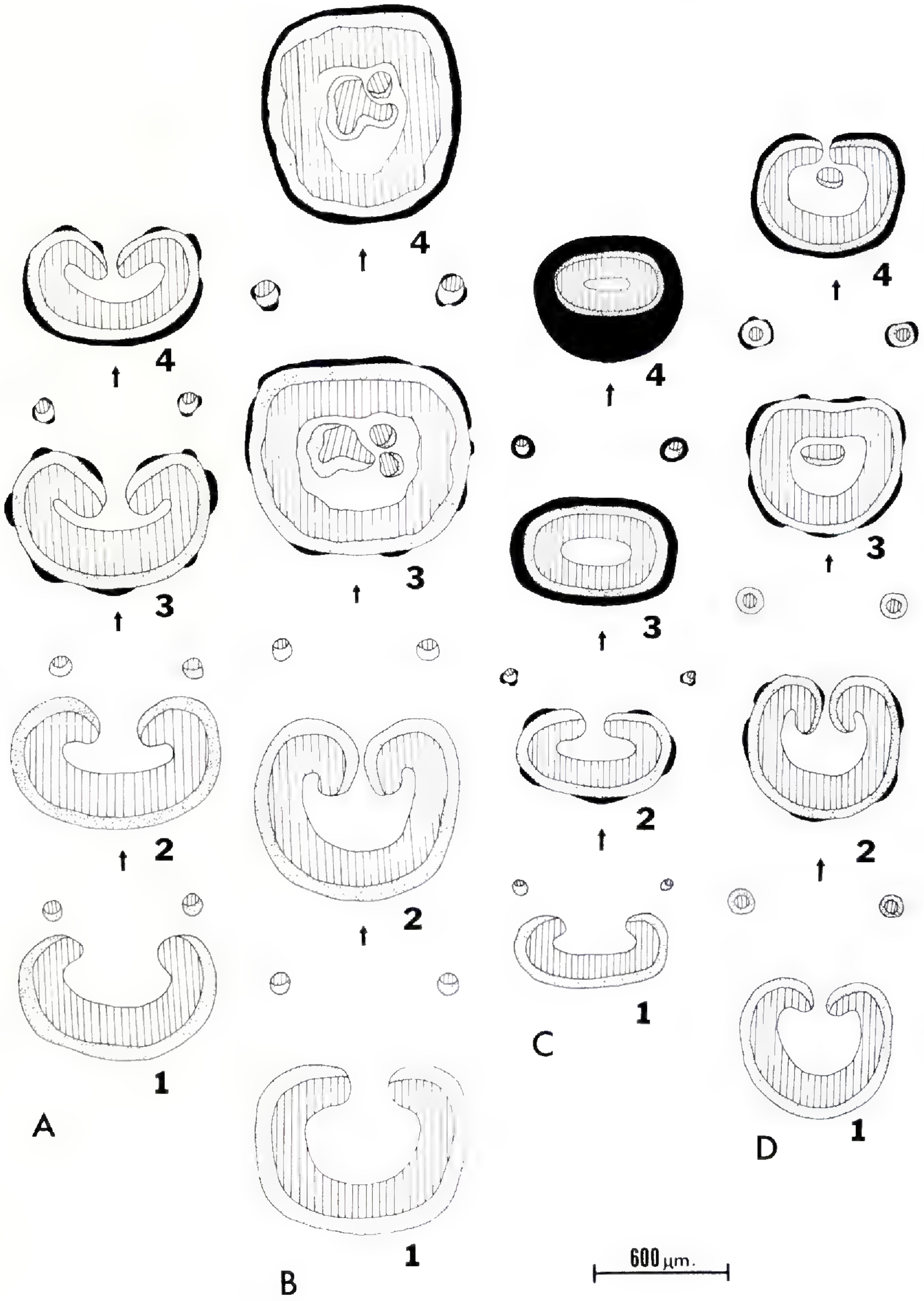

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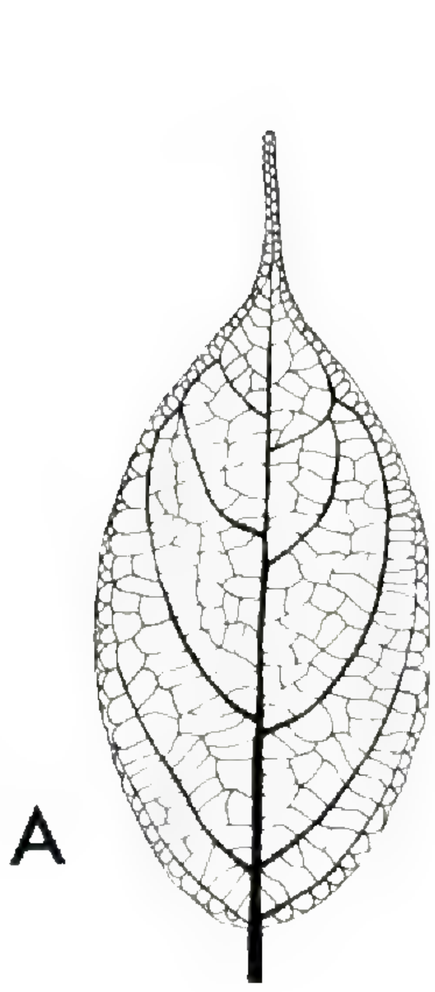
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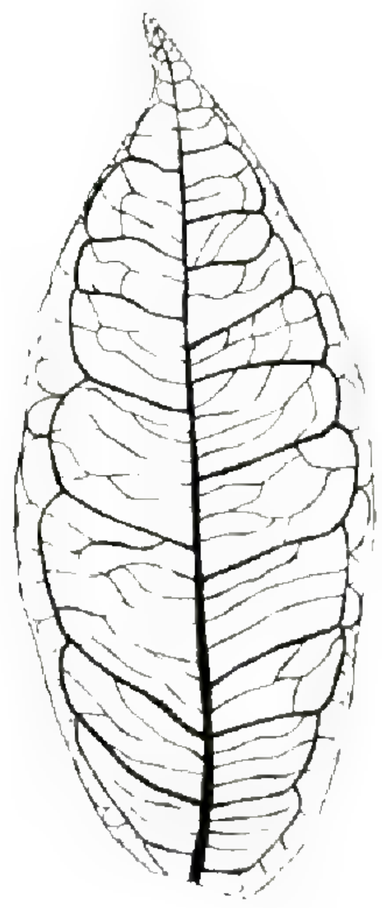
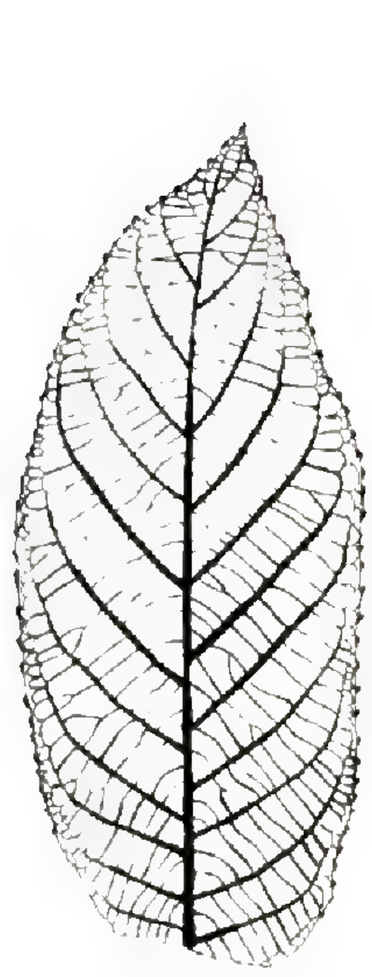

B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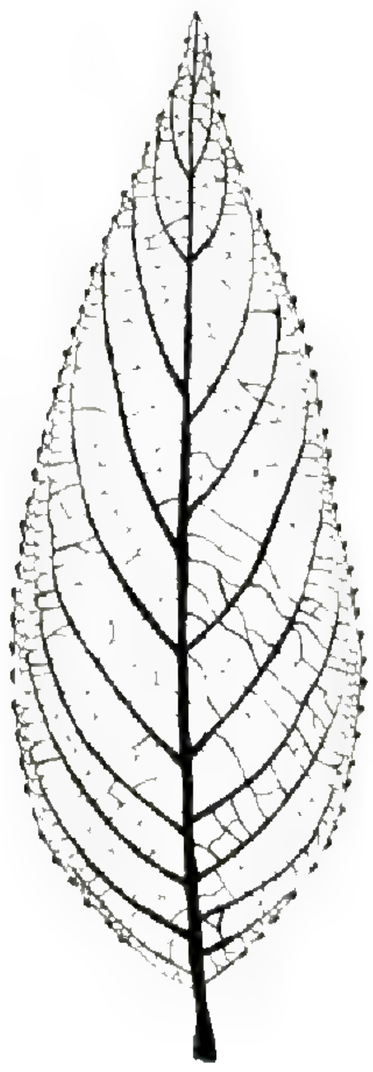
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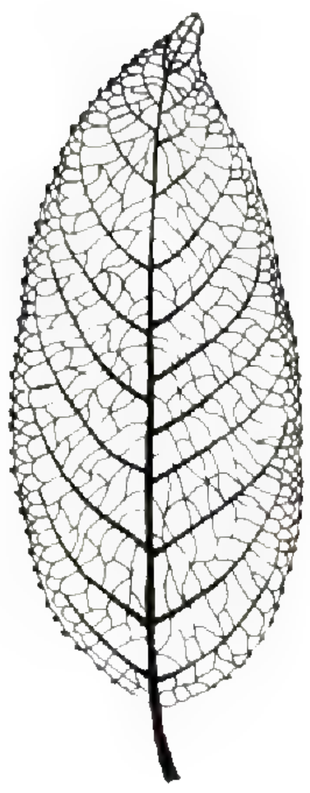
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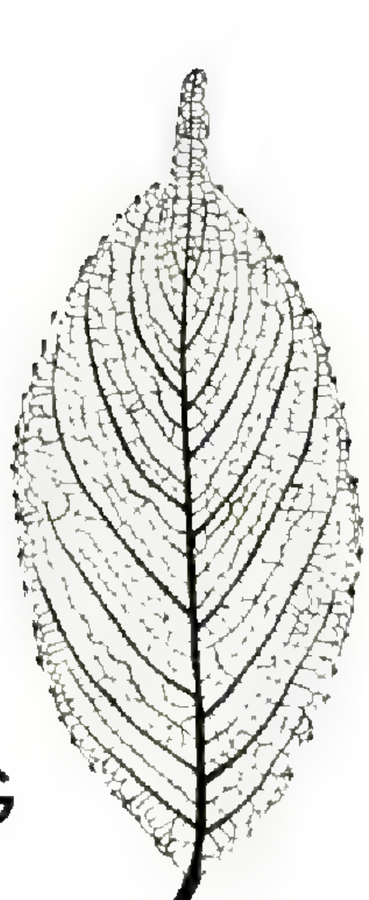
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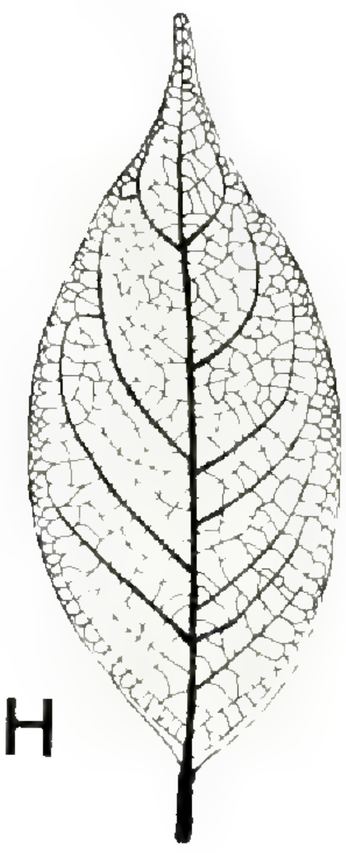
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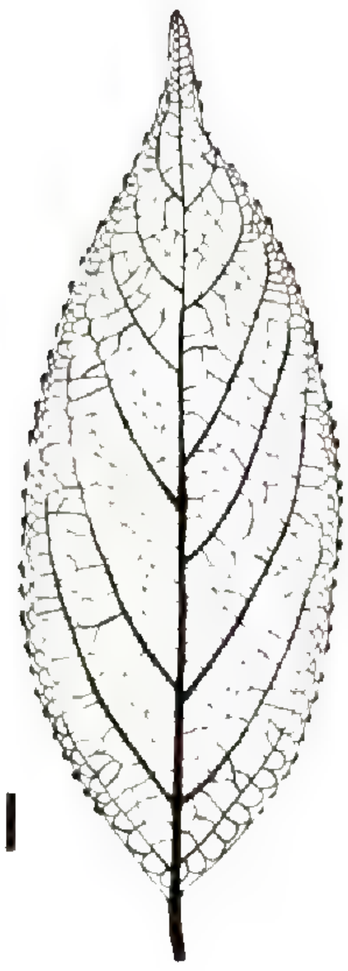
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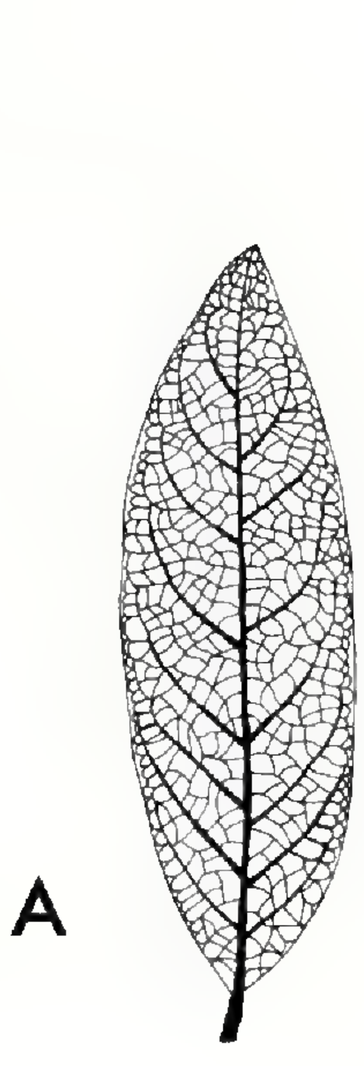
SCHADEL & DICKISON, LEAF ANATOMY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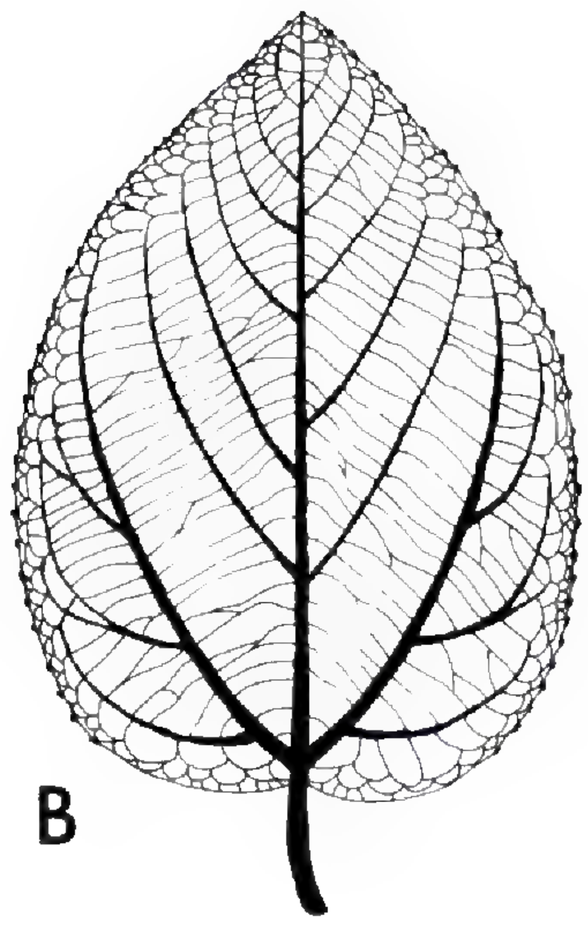
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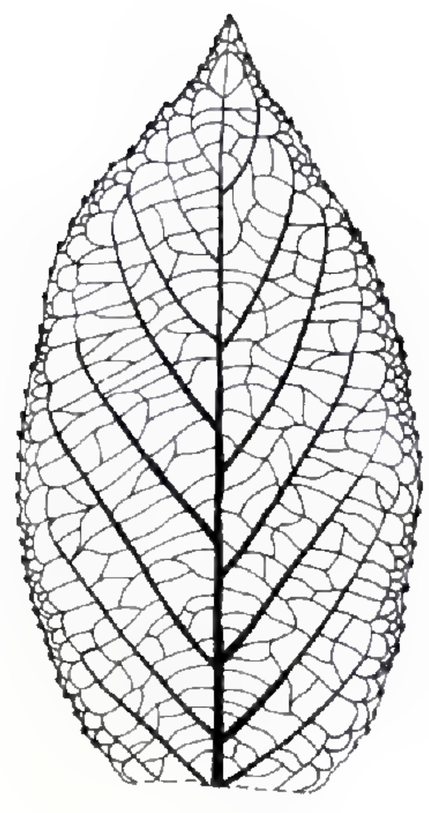
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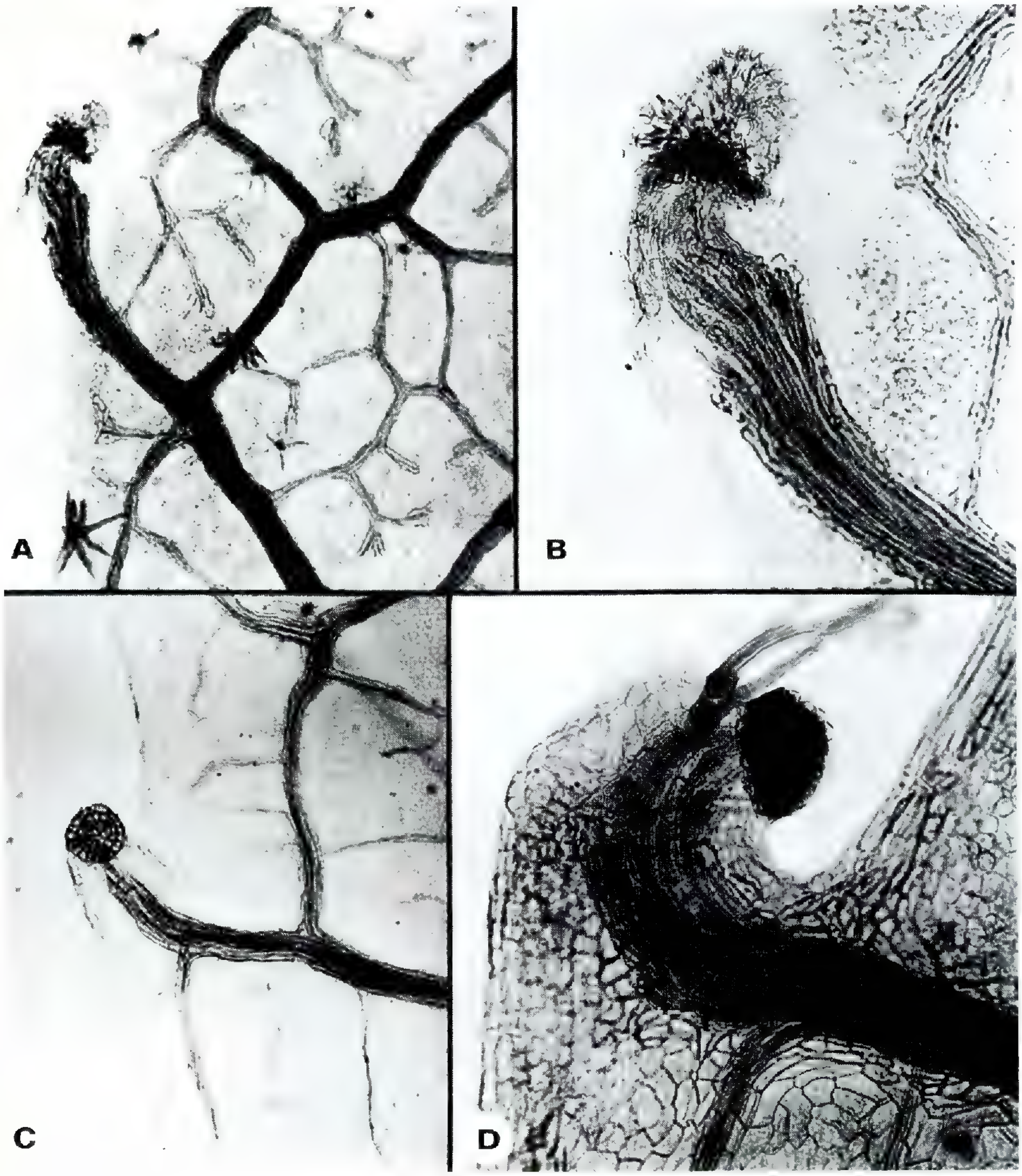

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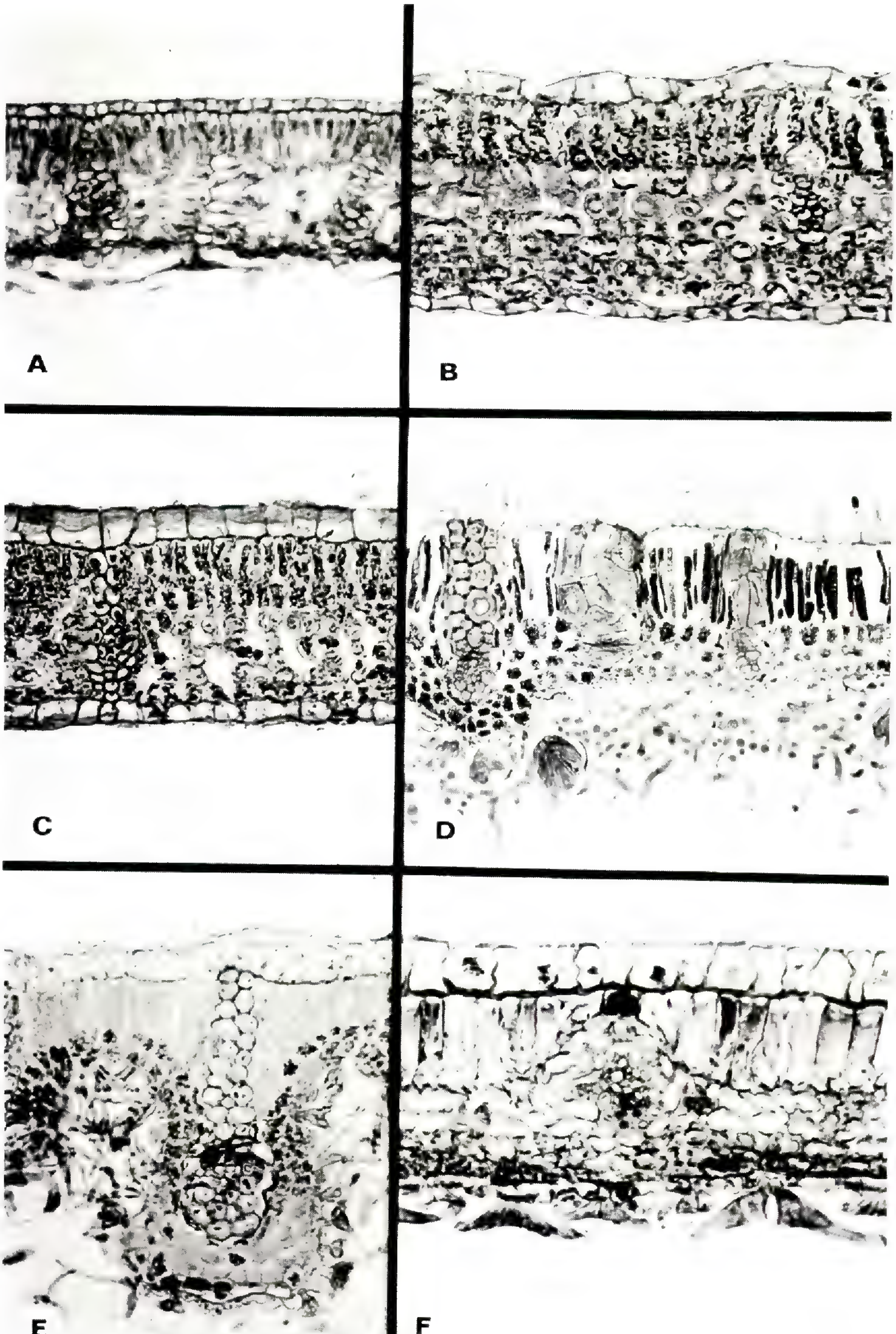

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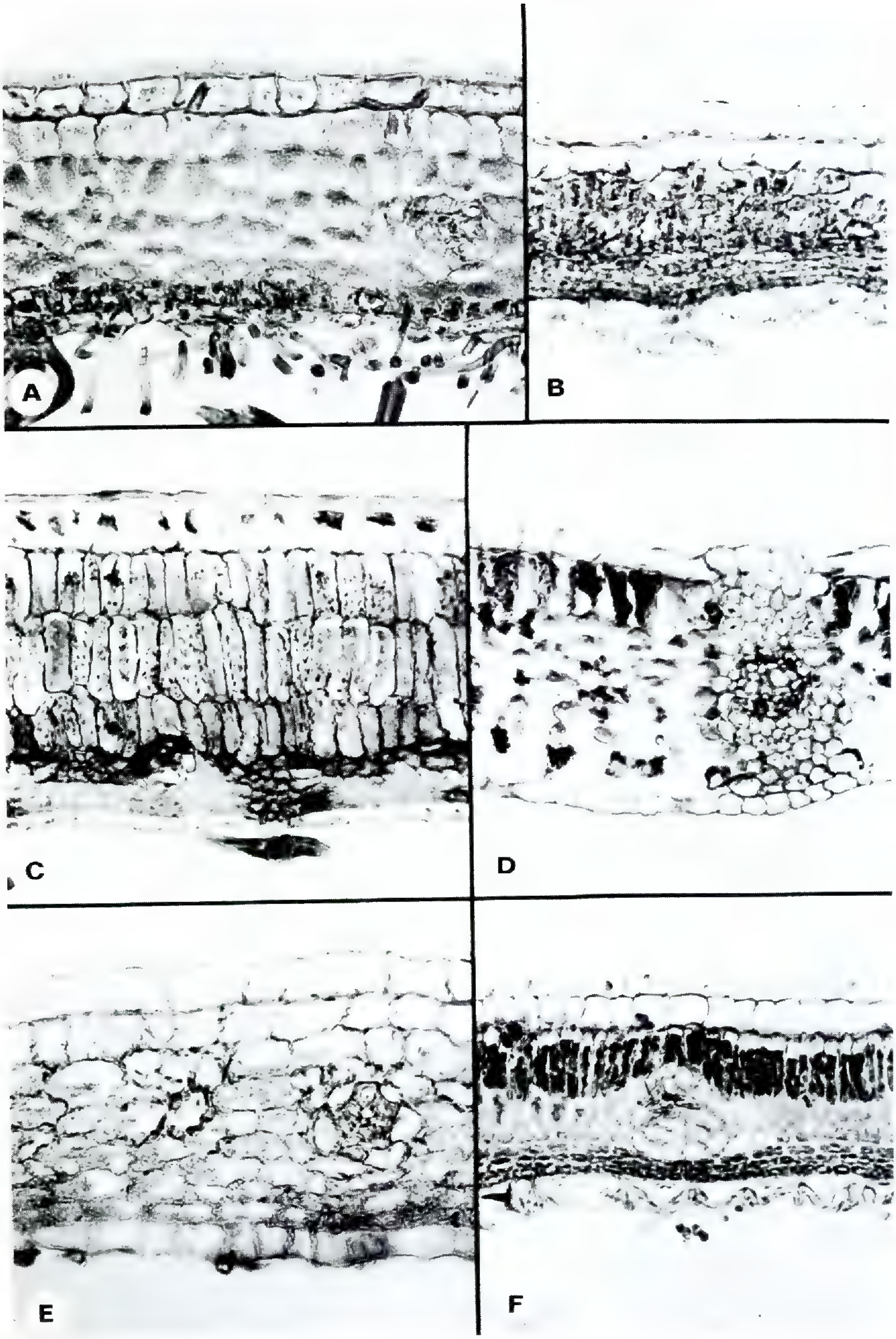


SCHADEL & DICKISON, LEAF ANATOMY

A REEXAMINATION OF PORTLANDIA (RUBIACEAE) AND ASSOCIATED TAXA [1]

ANNETTE AIELLO

THE OBJECTIVES of the present study have been to establish the generic limits of the genus *Portlandia*, to determine the position of taxa not properly assigned to it, to determine the number of species belonging to *Portlandia* and to describe them, and, finally, to reexamine all of the important taxa ever placed in the genus for additional characters that may have been overlooked or underrated by past workers.

DESCRIPTION OF THE FAMILY

The Rubiaceae, containing approximately 6000 species and over 600 genera, is the third largest family of dicotyledons. It is a mostly tropical group of trees, shrubs, climbers, and herbs, which with very few exceptions have opposite, stipulate leaves and sympetalous, epigynous flowers. The inflorescence is fundamentally a cyme and varies from a much-branched cymose panicle to an inflorescence reduced to a solitary flower. The corolla aestivation can be valvate, contorted, or imbricate. The fruit may be a capsule, a berry, a pyrene, or a schizocarp, and varies in number of locules and number of ovules per locule. Nectar is usually secreted by a gland around the base of the style. While heterostyly is common within the family, it is not found in all tribes. *Cinchona*, the source of quinine, and *Coffea*, the seeds of which are used to make coffee, are genera of economic importance. *Ixora*, an evergreen shrub or small tree with red, orange, yellow, or white flower clusters, and *Gardenia*, with scented white flowers, are frequently cultivated in warm climates as ornamentals. According to information gathered from Willis (1973), about 37 percent of the genera are monotypic. This high incidence may be due to a lack of understanding of the essential generic characters within the family; more likely, it may indicate that rapid evolution took place in the family at some time in the past and was followed by widespread extinction, leaving many genera isolated from their near relatives and resulting in a group that is, at the same time, clearly natural and extremely diverse. A major problem within the family has been that it contains a great many genera that resemble each other superficially, although when minute but very basic characters are examined, they may prove to be unrelated and even to belong to different tribes.

[1] Extracted from a thesis submitted by Annette Aiello to the Department of Biology, Harvard University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

HISTORY OF CLASSIFICATION WITHIN THE RUBIACEAE

In 1763 Adanson divided the Aparines, as he called the group of taxa now known as the Rubiaceae, into two sections based on the number of ovules in their fruits. Section I, with two ovules, included seventeen genera, and section II, with more than two ovules, included fourteen. With a total of only thirty-one genera known, and with those so evenly divided as to the number of ovules, his classification seems an almost natural one based on information available at the time.

Twenty-six years later, Jussieu (1789) used the name Rubiaceae when he published a classification more elaborate than that of Adanson. In it he recognized four main groups of genera instead of two: 1) fruit didymous (based on *Rubia*), 2) fruit with two ovules (based on *Coffea*), 3) fruit with many ovules (based on *Cinchona*), and 4) fruit with many locules (based on *Guettarda*). In addition, Jussieu recognized subdivisions of these taxa based on the number of stamens (4, 5, 6, or more), on whether the leaves were whorled or opposite, and on whether the flowers were aggregated or not. Although the systems of Adanson and Jussieu were simple and easy to use, they cut through now-accepted tribes and even genera and are thus no longer usable.

Since the time of Adanson and Jussieu, new genera have been added to the Rubiaceae at the rate of almost 2.5 per year, yet until recently (Verdcourt, 1958; Bremekamp, 1966) no important advances toward a really natural classification of the family had been made. Adanson's system of sections (equivalent in rank to subfamilies) has been followed almost exclusively in major treatments of the family (de Candolle, 1830; Richard, 1830; Endlicher, 1838; Schumann, 1891). De Candolle (1830) and Richard (1830) based tribes on the degree of dryness or fleshiness of the fruits, a division that also tends to cut through natural groups. Bentham and Hooker's (1873) proposed division into three series represented a compromise between the systems of Adanson and Jussieu.

The first step toward a more natural classification was taken by Verdcourt (1958), who proposed the division of the family into three subfamilies based on a number of correlated characters, especially presence or absence of raphides, multicellular uniseriate vs. unicellular nature of the hairs, and presence or absence of albumin in the seeds. In addition, he used habit, aestivation of the corolla, presence or absence of heterostyly, shape of the stigma, number of ovules per locule, and testa sculpturing. Although Bremekamp (1966) divided the family into eight subfamilies, his classification and that of Verdcourt are in basic agreement on most major issues. They both recognize three main subfamilies (Rubioideae, Cinchonoideae, and Guettardoideae), but Bremekamp also splits off five smaller subfamilies based on the presence of such unique characters as the ixoroid pollination mechanism, where the style acts as a pollen receptacle before becoming receptive itself; hair tufts on the seeds; or styloides (columnar crystals in cells). While these systems represent a large advance toward a more natural classification within the family, it

will doubtless be a long time before basic relationships are well understood.

In general, recent workers distinguish tribes by such characters as habit, presence or absence of spines, stipule shape and size, perfect or dioecious flowers, inflorescence type, corolla aestivation, corolla symmetry, stamen insertion, stigma shape, number of ovules per locule, ovule attachment, dehiscence or indehiscence of fruit, degree of dryness or fleshiness of fruit, and whether seeds are alate or exalate. Much work remains to be done at the tribal level in the areas of palynology, wood anatomy, and fruit and seed morphology, where further information may yield characters of taxonomic value.

POSITION OF THE CONDAMINEEAE

The tribe Cinchoneae was designated by Richard (1830) as including plants with dry, 2-locular, many-seeded fruits, opposite leaves, and interpetiolar stipules. As redefined by later workers, the Cinchoneae retained only those taxa with seeds both winged and vertical or ascending. In this tribe all three types of corolla aestivation (valvate, contorted, and imbricate) occur. Two tribes that resulted from splitting the Cinchoneae were the Rondeletieae and the Condamineeae (which contains the genus *Portlandia*). In both of these tribes the seeds are exalate and horizontal. Corolla aestivation is valvate in the Condamineeae, and contorted or imbricate in the Rondeletieae. While at first glance these three tribes appear well separated, pollen and wood studies indicate that this may not be the case. Verdcourt (1958, 1976) has simplified matters to some degree by including the Condamineeae in the Rondeletieae. The result, however, is a second tribe containing all three aestivation types. A clearer understanding of these three tribes could undoubtedly be obtained if they were simultaneously revised after careful study of fruit, seed, pollen, and wood characters.

Within the Condamineeae a variety of characters have been used to separate genera. These include shape, size, and persistence of stipules and calyx lobes, position of stipules, number of corolla lobes, shape of corolla tube in cross section, position of stamen insertion, type of anther dehiscence, and type of capsule dehiscence.

HISTORY OF THE GENUS PORTLANDIA

The genus *Portlandia* was first described by Patrick Browne (1756) in his *Civil and Natural History of Jamaica*. There he used a polynomial to describe "the large-leaf'd *Portlandia*," but did not assign a Latin epithet. It is clear from his description and untitled illustration (*t. xi*) that the plant he had in mind was *Portlandia grandiflora*, later briefly described, named, and credited to him by Linnaeus (1759), who also cited *t. 11*, in the tenth edition of *Systema Naturae*. Since neither worker mentioned a specimen, and because Linnaeus cited *t. 11*, that illustration must be the holotype although it was mistakenly engraved with six stamens instead

of five. This error was corrected in the 1789 edition of Browne's book, where the engraving was labeled *Portlandia grandiflora*.

Portlandia was named by Patrick Browne in honor of Margaret, Duchess of Portland and patroness of natural history. The name *Portlandia* was also applied in her honor to a genus of clams (Mollusca: Pelecypoda) by Mörch (1857).

Portlandia grandiflora, with its large, showy flowers, was well known to early workers. Aiton (1789) included it in his *Hortus Kewensis* (1: 228) and noted that it was introduced into cultivation in England in 1775 by a Mr. Ellis. The plant was illustrated in Curtis's *Botanical Magazine* (*t. 286.* 1795) and in Jacquin's (1763) *Selectarum Stirpium Americanarum Historia* (*t. 44*). It is represented in the Ware Collection of Glass Flowers at Harvard University by glass model no. 565, created by L. and R. Blaschka (1895) in Hosterwitz, Germany.

Portlandia was among the very earliest genera included in the Rubiaceae and was one of 31 genera listed by Adanson (1763) in his influential treatment of the family. Being both an early genus and one with showy flowers, *Portlandia* almost naturally became a catchall for other rubiaceous plants with large flowers. Superficial characters had a great deal of influence on how plants were classified, and it was only gradually that more basic characters such as fruit type and seed arrangement were considered important. *Portlandia* became a temporary resting place for quite a number of plants. By 1889 it included ten species, only three of which truly belonged there. In 1918 the genus reached its largest size — 21 species. Taxa have been removed periodically as old generic limits have been more clearly defined and new genera recognized. At one time or another *Portlandia* has included various taxa now assigned to *Coutarea*, *Bikkia*, *Exostema*, *Siemensia*, *Coutaportla*, *Schmidtottia*, and *Hintonia*.

GENERA PREVIOUSLY SEPARATED FROM PORTLANDIA. Plants having axillary flowers, straight corolla tubes, unflattened capsules, and wingless seeds were recognized by Aublet (1775) as *Portlandia*. Plants having terminal flowers, gibbous corolla tubes, strongly flattened capsules, and winged seeds were considered distinct from *Portlandia*, and Aublet based the tropical American genus *Coutarea* on them. Unfortunately, he applied a new epithet (*speciosa*) instead of the previously used *hexandra*, and not until 1889 was the taxon correctly named *Coutarea hexandra* (Jacq.) Schumann. At present, *Coutarea* is in need of revision, and the number of species in the genus is uncertain.

In 1923 Urban named three new genera, *Siemensia*, *Coutaportla*, and *Schmidtottia*, based on plants originally described as *Portlandia*. He distinguished the monotypic *Siemensia* (endemic to Cuba) on the basis of leaf anatomy. Its leaves have resin-producing secretory cells as well as raphides and lack crystal sand (calcium oxalate) and the typical palisade and spongy mesophyll layers. In contrast, *Portlandia* leaves lack secretory cells and raphides but have both crystal sand and the typical palisade and spongy mesophyll layers. Urban separated *Coutaportla* (also monotypic;

endemic to Mexico) from *Portlandia* based on a number of characters: flowers 4-merous vs. 5- to 7-merous; calyx tube compressed vs. terete; capsule septicidal vs. loculicidal; placentae subquadrate and attached only to middle of septum vs. linear and attached to septum for its whole length; ovules few and not completely covering placentae vs. many and covering placentae; seeds unappendaged vs. appendaged (funicle persistent); and stipule margins denticulate vs. entire. *Schmidtottia* (ten species endemic to Cuba) was distinguished as having terminal inflorescences, septicidal capsules, oval placentae that are attached only to the middle of the septum, unappendaged seeds, and stipules that are truncate and connate into a sheath (as opposed to triangular and distinct).

PROPOSED CLASSIFICATION OF PORTLANDIA. The genus *Portlandia* (Rubiaceae) as redefined in this study is endemic to the island of Jamaica and comprises five species. Of the more than thirty taxa formerly included in *Portlandia*, sixteen still remained at the outset of the present study. Of these sixteen, only five are here accepted as *Portlandia*, four represent the three new genera *Cigarrilla*, *Cubanola*, and *Thogsennia*, one is assigned to *Coutarea*, three belong in *Isidorea*, two are conspecific with *P. platantha*, and one remains unassigned to a genus until the fruits are known. In addition, two other new genera, *Ceuthocarpus* and *Osa*, are separated from *Schmidtottia* and *Hintonia*, respectively. For a complete list of taxa associated with *Portlandia*, see TABLE 1.

TABLE 1. **List of taxa associated with Portlandia.**

Ceuthocarpus Aiello.
  C. involucratus (Wernham) Aiello.

Cigarrilla Aiello.
  C. mexicana (Zucc. & Martius ex DC.) Aiello.

Coutaportla Urban, Symb. Antill. **9:** 146. 1923.
  C. ghiesbreghtiana (Baillon) Urban, *ibid.* 147.

Coutarea Aublet, Pl. Guian. **1:** 314. 1775.
  C. hexandra (Jacquin) Schumann in Martius, Fl. Brasil. **6**(6)**:** 196. 1889.

Cubanola Aiello.
  C. daphnoides (R. Graham) Aiello.
  C. domingensis (Britton) Aiello.

Hintonia Bullock in Hooker's Ic. Pl. **33:** 1. 1935.
  H. latiflora (Sessé & Moç. ex DC.) Bullock, *ibid.* 4.
  H. lumaeana (Baillon) Bullock, *ibid.* 5.

Isidorea A. Richard ex DC. Prodr. **4:** 405. 1830.
  I. brachycarpa (Urban) Aiello.
  I. oblanceolata (Urban) Aiello.
  I. polyneura (Urban) Aiello.

Schmidtottia Urban, Symb. Antill. **9:** 137. 1923.
  S. elliptica (Britton) Urban, *ibid.* 139.

S. nitens (Britton) Urban, *ibid.* 141.
S. sessilifolia (Britton) Urban, *ibid.* 142.
S. sessilifolia subsp. *shaferi* (Standley) Borhidi, Bot. Kozlem. **58:** 176. 1971.
S. uliginosa (Wernham) Urban, Symb. Antill. **9:** 139. 1923.

Siemensia Urban, Symb. Antill. **9:** 143. 1923.
S. pendula (Wright) Urban, *ibid.* 145.

Thogsennia Aiello.
T. lindeniana (A. Richard) Aiello.

MORPHOLOGY

Leaves

Many of the leaf characters discussed below are summarized in Table 2.

The leaves of the 12 genera studied are all typical of the Rubiaceae in that they are opposite, simple, entire, and stipulate. Exceptions are *Ceuthocarpus involucratus* and *Schmidtottia cubensis*, with leaves arranged two or three per node.

Six genera (*Ceuthocarpus, Cigarrilla, Coutaportla, Isidorea, Portlandia,* and *Schmidtottia*) have coriaceous leaves; those of some species of *Isidorea* are rigid and pungent as well. The leaves of *Coutarea, Hintonia, Cubanola, Osa, Siemensia,* and *Thogsennia* are chartaceous. When dry, the leaves of *Cigarrilla* and *Thogsennia* curl longitudinally; those of *Ceuthocarpus* and *Schmidtottia* are very dark (dark brown to black) above and much paler (green to pale brown) below.

The hairs on the leaves of *Ceuthocarpus* and *Schmidtottia* are simple (Figure 1), while those on the leaves of *Siemensia* (Figure 2) are uniseriate and have two to four cells each. In both types the hairs are usually surrounded at the base by a rosette of epidermal cells. The remaining nine genera have glabrous leaves, although in *Hintonia standleyana* the leaves are pubescent when young.

The venation in all cases is brochidodromous (as defined by Hickey, 1973) or co-arcuate (as defined by Melville, 1976), depending upon whose terminology is used. The secondary veins are alternate, with four to seven pairs per leaf, except in *Isidorea* where they range from ten to thirty in number and are closely packed together. The venation of *Isidorea* approaches Melville's (1976) definition of "paxillate," but the arches formed by successive secondary veins are still evident. In a number of species of *Isidorea,* the very numerous higher order veins are not restricted to a single plane and almost entirely fill the thick leaves.

Several species of *Portlandia* and *Schmidtottia,* as well as one of *Isidorea,* have sessile leaves; the rest have petioles of varying length.

The largest leaves are found in *Cubanola, Osa, Portlandia,* and *Thogsennia;* those of the other genera are intermediate to small in size.

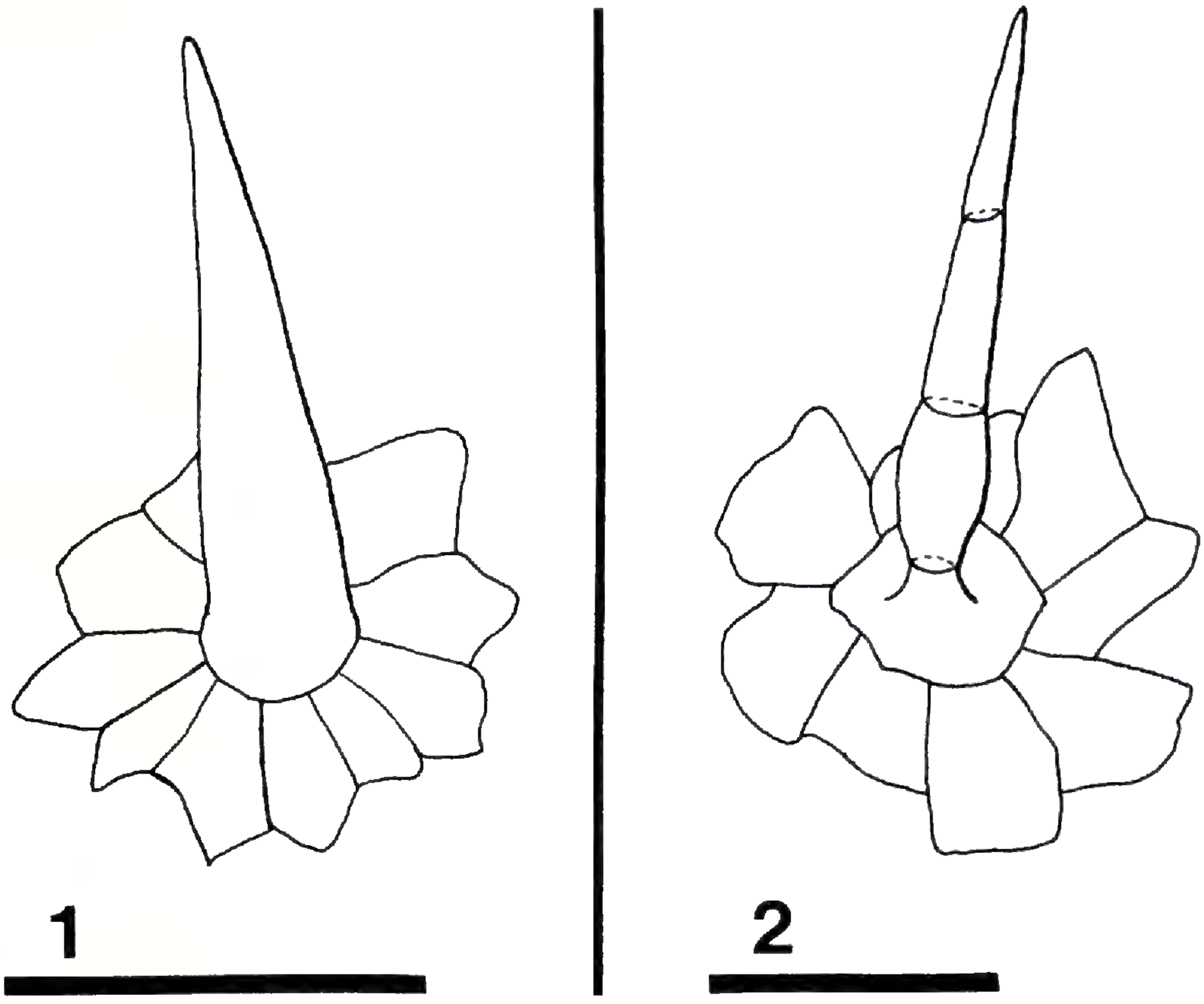
Leaf shape is quite variable, ranging from linear-lanceolate through elliptic, ovate, and obovate, to nearly circular. The apices vary from long-

TABLE 2. Summary of leaf shape and size in Portlandia and associated genera.

GENUS	PETIOLE LENGTH (mm.)	BLADE SHAPE	BLADE LENGTH (cm.)	BLADE WIDTH (cm.)	BLADE APEX	BLADE BASE
Ceuthocarpus	5–13	narrowly elliptic to elliptic-obovate or narrowly obovate	2–6	0.6–2.5	rounded	acute to attenuate
Cigarrilla	3–5	oblong	3.5–6.5	1.6–2	acute, mucronate	obtuse to acute
Coutaportla	2–3	elliptic	2–3	0.9–1.3	acute	acuminate
Coutarea	7–10	ovate to elliptic	4–10	1.9–5	acuminate	acute to obtuse
Cubanola	2–15	ovate, elliptic-oblong, or elliptic	6–18	2.5–8.8	acute to acuminate	acuminate to acute, or obtuse
Hintonia	11–18	widely elliptic, ovate, narrowly lanceolate, or oblong-lanceolate	4.5–9	2.5–4	acute to acuminate	acute
Isidorea	0–7	elliptic, linear-lanceolate, oblanceolate, or obovate	1–12	0.3–6	acute, obtuse, rounded, or gradually acuminate; pungent	rounded, obtuse, narrowing to base, acute, or acuminate
Osa	7–12	elliptic or narrowly oblong	16.5–19	4.7–5.7	long-attenuate	long-attenuate
Portlandia	0–10	ovate, narrowly elliptic, elliptic, widely elliptic, circular, or obovate	6–22	2.5–14	rounded, obtuse, acute, or acuminate	attenuate, acuminate, acute, obtuse, or cordate
Schmidtottia	0–5	circular, elliptic, oblong-lanceolate, or obovate	1–11	0.2–6.5	rounded, obtuse, acute, or gradually acuminate	rounded, obtuse, acute, narrowed, subcordate, or cordate
Siemensia	6–10	elliptic or oblong-elliptic	3.5–5.5	1.6–3	acute to acuminate	acute to obtuse
Thogsennia	8–10	elliptic-lanceolate or oblong-lanceolate	12–19	4.5–6.5	acute to acuminate	acute

attenuate through acute and obtuse to rounded, and the bases from attenuate through acute and obtuse to cordate.

Epidermal cell anticlinal walls are undulate in *Hintonia, Isidorea, Portlandia*, and *Osa*, and slightly undulate to straight in the remaining genera.



FIGURES 1, 2. Leaf hairs: 1, *Schmidtottia elliptica* (*León 21131* (NY)); 2, *Siemensia pendula* (*Shafer 13411* (NY)). Bar scales = 0.1 mm.

The stomata in all cases are paracytic, although the number of subsidiary cells varies from two in *Cigarrilla, Coutaportla, Coutarea, Hintonia*, and *Portlandia*, and two to three in *Cubanola, Isidorea*, and *Thogsennia*, to two to four in *Siemensia*, and four in *Ceuthocarpus, Osa*, and *Schmidtottia*. In *Siemensia* the guard cells are often sunken and difficult to see.

Druse crystals were noted in cleared leaves of *Cigarrilla, Hintonia, Isidorea, Portlandia, Siemensia*, and *Thogsennia*. Bundles of raphide crystals were found in the leaves of *Siemensia*. Leaves of *Osa* were not available for clearing.

A red substance occurs in leaf cells of *Ceuthocarpus, Coutarea, Schmidtottia*, and *Siemensia*; however, the exact location of those cells was not determined.

A study of leaf anatomy for the 12 genera covered here, and a general survey of leaf anatomy for the family Rubiaceae, would doubtless be a most profitable undertaking and might help to clarify tribal and generic relationships. Indeed, Urban (1923), when describing the genus *Siemensia* as distinct from *Portlandia*, did so on the basis of leaf anatomy.

NODES

Sinnott (1914) stated that, "The Rubiaceae are overwhelmingly unilacunar, the only exception observed being the genus *Sarcocephalus*. . . ." Howard (1970), after his survey of nearly ninety genera (pers. comm.) in the Rubiaceae, reported trilacunar nodes in twelve genera (including *Portlandia*) representing eight tribes of that family. Further work in the Rubiaceae may reveal that the unilacunar node is the predominant type in the subfamily Rubioideae (*sensu* Bremekamp, 1966), with both nodal types being common in the Ixoroideae and Cinchonoideae (Howard, unpublished data).

Material of *Coutaportla*, *Cigarrilla*, and *Portlandia* (seedlings) was examined for nodal type.

In *Coutaportla* the nodes are unilacunar, with the single crescent-shaped trace giving off stipule traces just before it enters the petiole. From there it continues as a single trace to the base of the blade.

Cigarrilla has trilacunar nodes, with the lateral traces leaving the stele at a point almost 10 mm. below the attachment of the leaves, while the median trace does not leave until immediately before it enters the petiole. It is at this later point that the lateral traces converge into the ends of the median trace, with portions going to the stipules. Within the petiole base the traces separate again and continue the full length of the petiole as a crescent-shaped trace plus two rib traces.

Portlandia also has trilacunar nodes (Howard, 1970), but differs from *Cigarrilla* in that the three traces leave the stele at approximately the same level.

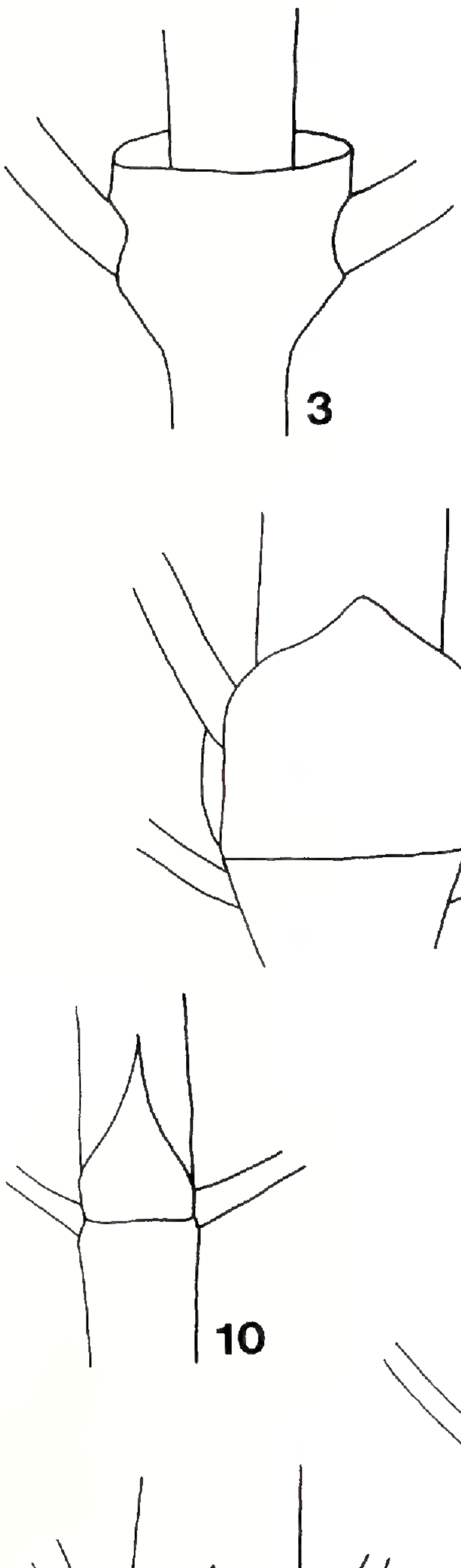
Examination of *Portlandia grandiflora* seedlings revealed that each of the opposite cotyledons is supplied with two traces from one gap, a pattern previously reported (Thomas, 1907) for seedlings of many dicotyledons.

STIPULES

Among the Sympetalae only members of the Rubiaceae have stipules as a constant character. These may be interpetiolar, intrapetiolar, or sheathing. By far the most common type for the family is the interpetiolar stipule. Often within this type, the adjacent members of the two pairs are united along their outer margins, resulting in two interpetiolar stipules per node.

Among the twelve genera studied, *Schmidtottia* has truncate sheathing stipules (FIGURE 3), *Ceuthocarpus* has intrapetiolar erose stipules (FIGURE 4); the other ten genera have triangular ones. In all genera except *Coutaportla*, in which the stipules are free from each other, the two stipules at each node are at least slightly connate at their bases and thus encircle the stem.

In *Coutaportla* (FIGURE 5) and *Hintonia* (FIGURE 6) the stipules are acute, while in *Portlandia* (FIGURE 7) they are acute or obtuse. *Cigarrilla*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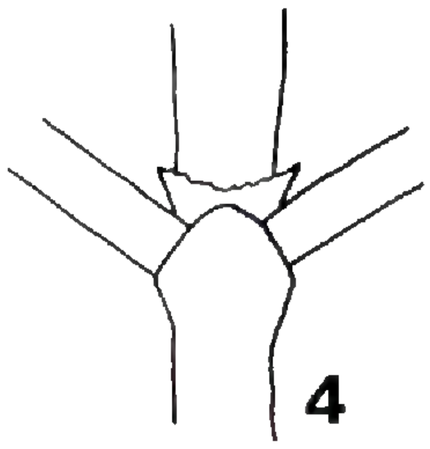
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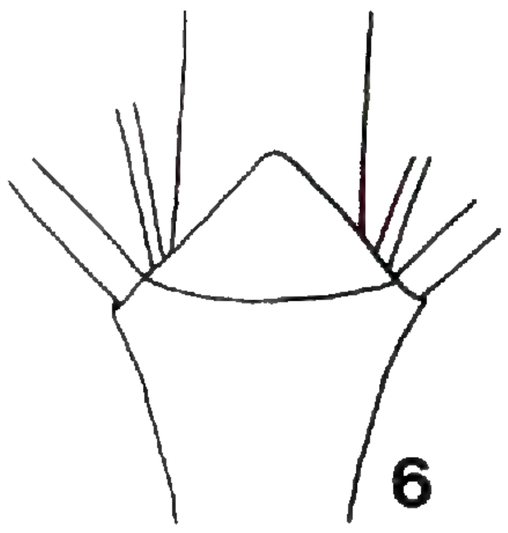
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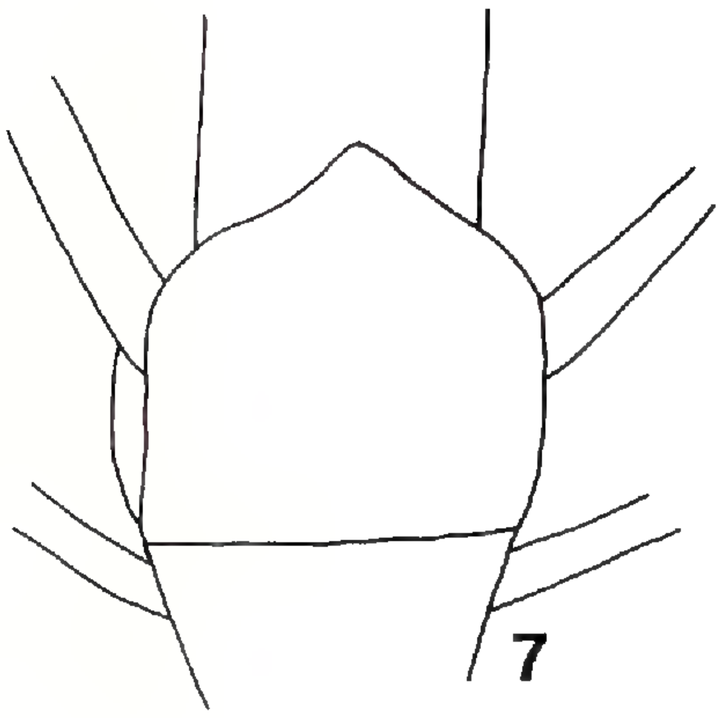
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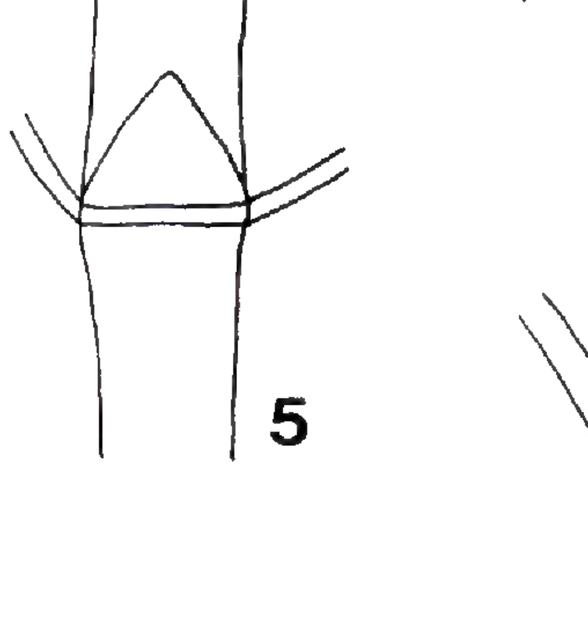
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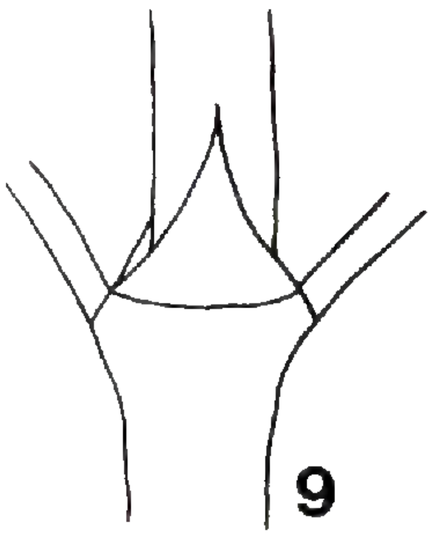
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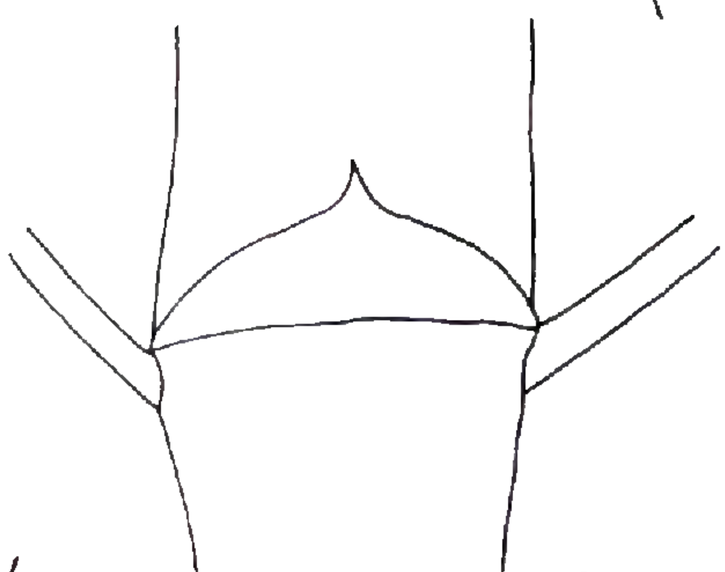
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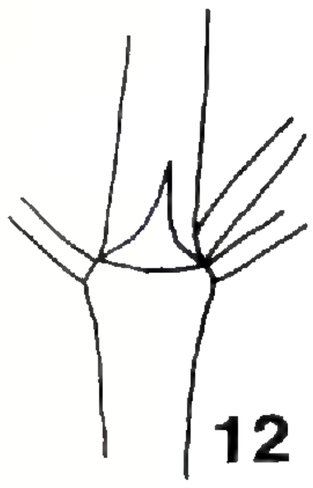
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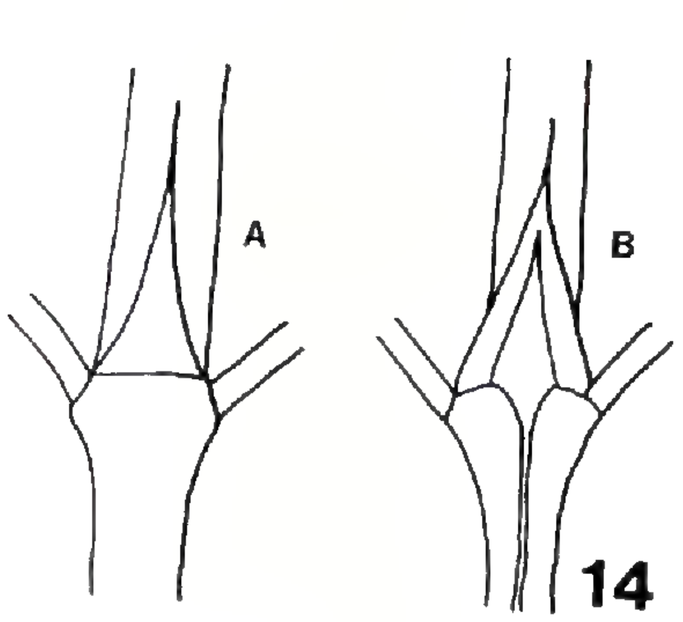
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FIGURES 3–14. Stipules: 3, *Schmidtottia nitens*; 4, *Ceuthocarpus involucratus*; 5, *Coutaportla ghiesbreghtiana*; 6, *Hintonia latiflora*; 7, *Portlandia microsepala*; 8, *Cigarrilla mexicana*; 9, *Coutarea hexandra*; 10, *Cubanola domingensis*; 11, *Osa pulchra*; 12, *Siemensia pendula*; 13, *Thogsennia lindeniana*; 14, *Isidorea leptantha*: A, before splitting; B, after splitting. Bar scale = 2 mm.

(FIGURE 8), *Coutarea* (FIGURE 9), *Cubanola* (FIGURE 10), *Osa* (FIGURE 11), *Siemensia* (FIGURE 12), and *Thogsennia* (FIGURE 13) have acuminate to attenuate stipules. *Isidorea* (FIGURE 14) differs from all the rest in having narrow, aristate stipules that eventually split from the base to the apex, giving the appearance of four stipules per node. At the same time, a groove opens in the stem, beginning just below each stipule and continuing down to the next node. This arrangement gives the branches a distinctive appearance. The stipules of *Cigarrilla* and *Coutarea* also occasionally split from the base to the apex with age, but these two genera lack the stem groove of *Isidorea*.

INFLORESCENCE

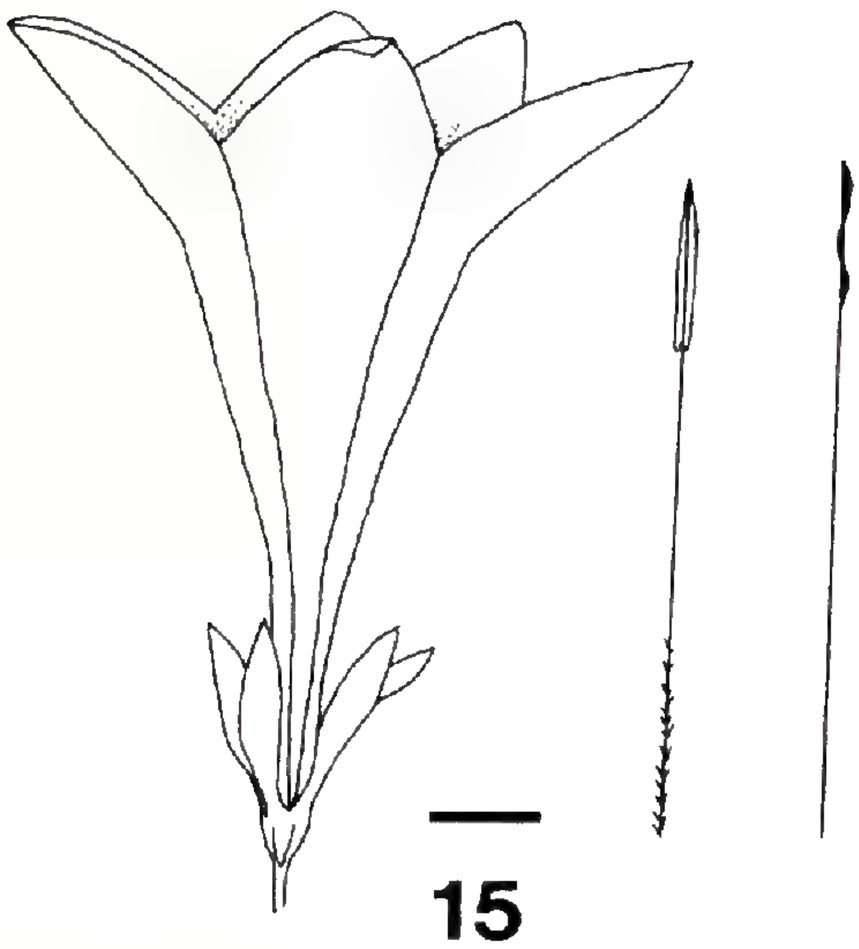
Within the Rubiaceae the inflorescence is typically cymose, with the most common condition being a much-branched cymose panicle. Solitary terminal flowers are rare.

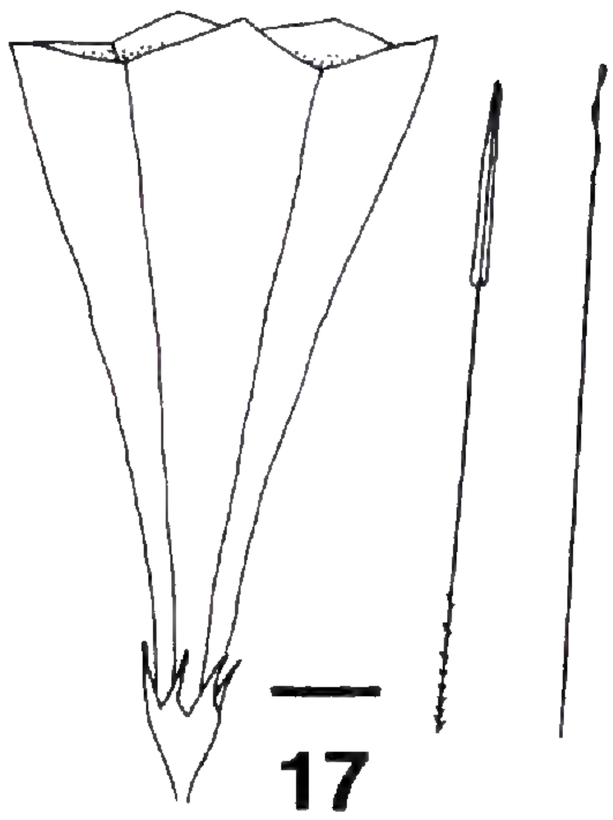
In *Ceuthocarpus*, *Coutaportla*, *Schmidtottia*, and *Siemensia* the inflorescences are terminal. *Ceuthocarpus* is unique among these in having solitary terminal flowers, each surrounded at the base by bracts and perhaps representing the terminal flower of a reduced cyme. In *Coutaportla* and *Schmidtottia* the flowers are in terminal simple or reduced cymes. In several species of *Schmidtottia* these cymes are condensed, with the sessile flowers crowded together. *Siemensia* inflorescences are terminal on axillary shoots. Typically, there are seven flowers, of which four arise from the axils of the upper two pairs of leaves, and three form a simple terminal cyme. After flowering, the leaves fall off the entire shoot, leaving a long-stalked panicle with seven stalked capsules.

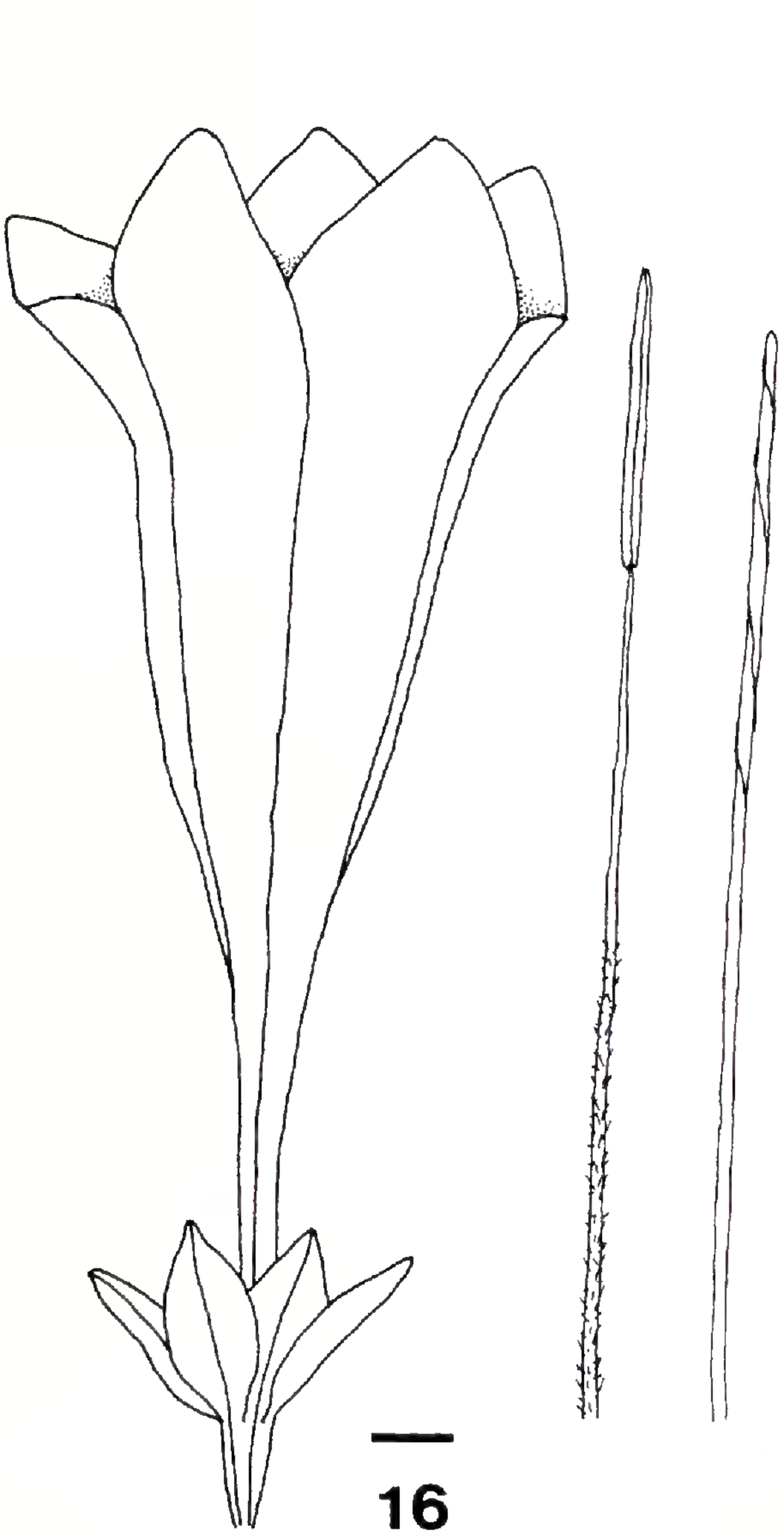
Cigarrilla, *Cubanola*, *Hintonia*, *Isidorea*, *Osa*, and *Thogsennia* have the flowers arranged one (rarely three) per axil in the upper one to four pairs of axils. *Isidorea* differs from the other genera in that three species (*I. brachyantha*, *I. leonardii*, and *I. leptantha*) have the flowers borne on axillary short shoots. Short shoots appear on occasional specimens of other *Isidorea* species as well. This genus needs field study with respect to its growth habits.

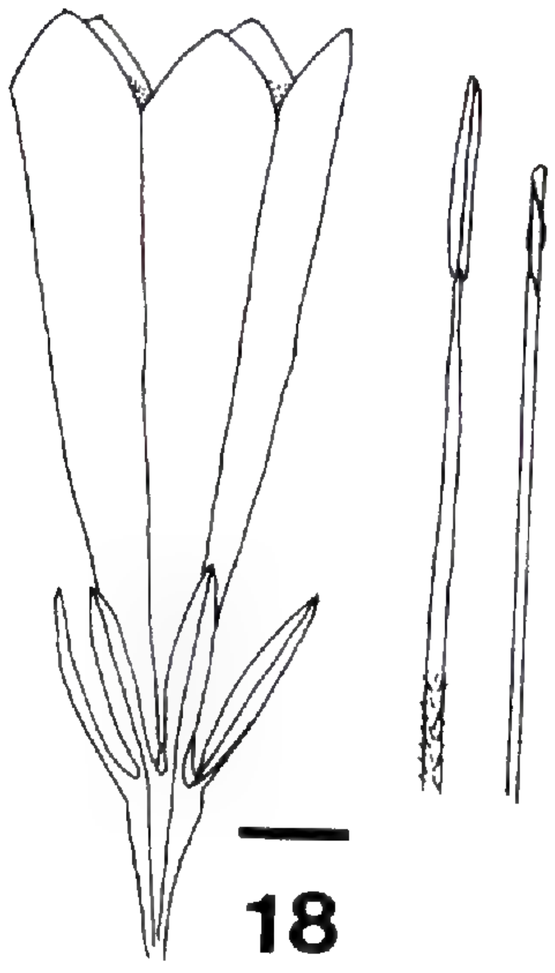
Portlandia and *Coutarea* have their flowers arranged in reduced cymes of one to six and one to three flowers per axil, respectively, in the upper one to four pairs of axils. In *Portlandia* there is variation in the degree of cyme reduction among the species. *Portlandia harrisii* has three to six flowers per axil in condensed cymes with pedicels 1–5 mm. long. *Portlandia coccinea* and *P. platantha* have reduced cymes with one to three (most commonly two) flowers per axil. *Portlandia grandiflora* has reduced cymes with one or two (most commonly one) flower(s) per axil. Often these single flowers bear an aborted bud near the base of the pedicel. *Portlandia microsepala* has one flower per axil.

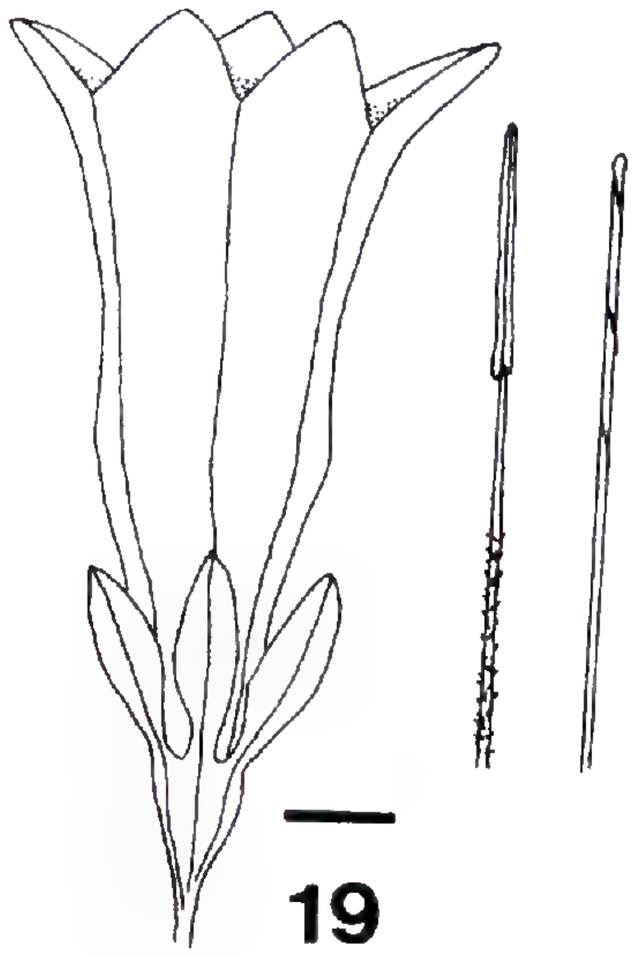
FLOWERS. While heterostyly is quite common in the Rubiaceae, it has not been reported for any genera within the Condamineeae and was not











FIGURES 15–19. Flowers, stamens, and styles: 15, *Portlandia platantha*; 16, *P. grandiflora* (*Adams 13213* (UCWI)); 17, *P. microsepala*; 18, *P. coccinea* (*Aiello 1308* (A)); 19, *P. harrisii* (*Aiello 1306* (A)). Bar scales = 10 mm.

found in any of the taxa included in this study. In all 12 genera examined, the stamens are attached to the basal 1 to 3 mm. of the corolla, and at anthesis both the style and the stamens reach to the sinus of the corolla lobes (except in *Hintonia*, *Coutarea*, and *Ceuthocarpus*, where they are exserted).

Few or no data on fragrance are available for *Ceuthocarpus*, *Isidorea*, *Osa*, *Schmidtottia*, or *Thogsennia*. Flower fragrance, where known, is associated with white or pink flowers.

Calyx, corolla, stamens, and style are discussed separately in the sections that follow. Flowers of all genera studied are pictured in FIGURES 15–31.

CALYX. In all 12 genera studied, the calyx lobes or sepals are joined only at the very base, and in all except *Coutarea* and *Coutaportla* (which have deciduous sepals) they are persistent or marcescent on the fruit.

The sepals of *Osa*, *Thogsennia*, and *Cubanola* are long (2–2.5 cm.) and subulate; those of *Hintonia* and *Coutarea* are shorter (0.7–1.5 cm.) but also subulate. *Cubanola* has keeled sepals, with the keels continuous with the wings of the capsule. The sepals of *Coutarea* are pubescent on their inner surface.

The sepals of *Ceuthocarpus*, *Siemensia*, and *Schmidtottia* are linear to subulate, while those of *Isidorea* are stiff, needle shaped, and keeled, each with a very sharp tip.

In *Cigarrilla* and *Coutaportla* the sepals are narrowly triangular. Each sepal of *Coutaportla* bears two or three red-tipped glands along each side near the base (FIGURE 32).

With the exception of *Portlandia microsepala*, which has subulate sepals 2–9 mm. long and 0.5 mm. wide, *Portlandia* has broader and thinner sepals than the other eleven genera studied. They are leafy and reach their largest size, 1.4–3.5 cm. long and 0.3–1.8 cm. wide, in *P. grandiflora*. The sepals of *P. coccinea*, *P. platantha*, and *P. harrisii* are lanceolate, linear to lanceolate, and elliptic, respectively, and are 0.7–2.5 cm. long and 2–7 mm. wide.

The calyx lobes of many of the taxa studied bear finger-shaped outgrowths on their adaxial surface near the base. Their structure is the same as that of the colleters commonly found on stipules in the Rubiaceae, and they are discussed under the heading "Colleters."

COROLLA. Many of the flower characters discussed below are summarized in TABLE 3.

The most common corolla color among the genera is white, although several genera also have pink, red, violet, or purple flowers. The only genus in which yellow flowers occur is *Schmidtottia*. Of the 12 genera studied, *Isidorea* and *Schmidtottia* offer both the most color variation and, together with *Coutaportla*, the smallest flowers.

In general, the larger-flowered species have funnelform corollas. Exceptions are *Osa*, with its long, trumpet-shaped flowers, and *Portlandia harrisii*, with large, narrowly bell-shaped ones. *Coutarea* is unusual among

TABLE 3. Summary of flower characters in Portlandia and associated genera.

GENUS	COROLLA COLOR	COROLLA SHAPE	NUMBER OF FLORAL PARTS	COROLLA LENGTH (cm.)	FRAGRANCE	COLLETERS ON CALYX
Ceuthocarpus	red	funnelform	5	3–3.5	?	–
Cigarrilla	white	funnelform	5	4.8–7.2	+	+
Coutaportla	white	funnelform	4	2–2.5	+	*
Coutarea	white or pink	funnelform; base curved and gibbous	5–6	(2–)5.2–7.3	+	+
Cubanola	white	narrowly funnelform	5	17.8–27.5	+	+
Hintonia	white	funnelform	6, 8	3–8	+	–
Isidorea	white, red-brown, rose, pale purple, or violet	tubular or funnelform	4–5	1.2–4	+ & ?	+ & –
Osa	white	trumpet shaped	5	26.5–27	?	+
Portlandia	white, pink, or red	funnelform, broadly funnelform, or narrowly bell shaped	5	2.9–22	+ & –	+ & –
Schmidtottia	ochroleucous, yellow, yellowish red, pink, red, or purple	funnelform, narrowly campanulate, or campanulate	5	1.4–5	?	–
Siemensia	white	funnelform	5	5.3–5.7	+	–
Thogsennia	white	narrowly funnelform	5	20–26.8	?	+

* Has glands on sepal edges, + = present, – = absent, ? = unknown.

rubiaceous plants in having zygomorphic flowers with the base of the corolla curved and gibbous.

A few taxa deviate from the usual condition of 5-merous flowers. These are *Coutaportla*, *Isidorea tetramera*, and *I. leonardii* (all 4-merous); *Ceuthocarpus* and *Coutarea* (both 5- or 6-merous); and *Hintonia* (6- or 8-merous).

Corolla length varies from 1.2 to 27.5 cm., with the smallest flowers found in *Isidorea*, *Schmidtottia*, and *Coutaportla*, and the largest in *Portlandia grandiflora*, *Cubanola*, *Thogsennia*, and *Osa*.

Corolla lobe aestivation for the tribe Condamineeae as a whole has been reported throughout the literature to be valvate. However, a search through published descriptions of the 12 genera included in this study yielded a variety of interpretations. Aestivation has been described for five genera: *Coutaportla*, narrowly imbricate (Urban, 1923); *Isidorea*, reduplicate valvate (Bentham & Hooker, 1873); *Portlandia*, reduplicate valvate (Bentham & Hooker, 1873), plaited-imbricative (Grisebach, 1861); *Schmidtottia*, induplicate imbricate (Urban, 1923); and *Siemensia*, narrowly quincuncially induplicate imbricate (Urban, 1923).

An examination of flower buds of *Portlandia*, *Isidorea*, *Cubanola*, *Cigarrilla*, *Siemensia*, *Hintonia*, *Coutarea*, *Thogsennia*, *Schmidtottia*, and *Coutaportla* revealed that all have imbricate aestivation of the corolla lobes. The width of lobe overlap varies from 1 to 3 mm. In all cases where the corolla is 5-merous, the imbrication is quincuncial. Flower buds of *Ceuthocarpus* and *Osa* were not available for study. Imbricate aestivation would place *Portlandia* and most of the genera associated with it in the Rondeletieae instead of the Condamineeae. Clearly, aestivation in the genera of these two tribes needs careful observation.

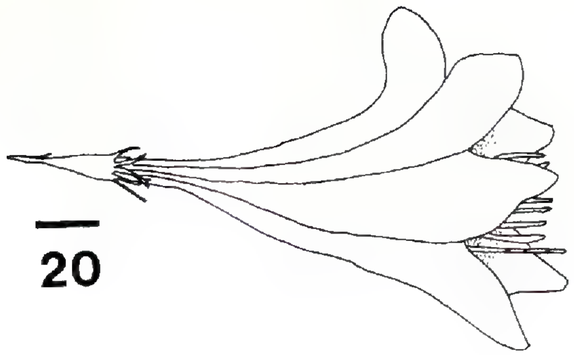
STAMENS, STYLE, AND STIGMA. In all genera studied, the number of stamens is equal to the number of corolla lobes. The stamens are connate for their basal 1 to 5 mm., forming a ring that is adnate to the basal 1 to 3 mm. of the corolla. The stamens and style reach to the sinus of the corolla lobes except in *Ceuthocarpus*, *Hintonia*, and *Coutarea*, where they are exserted 1 to 1.5 cm. The slender filaments are villous on their basal quarter to half, except in *Thogsennia*, where they are villous for almost three-quarters of their length, *Coutaportla*, where they are villous for their entire length, and *Osa*, where they are glabrous.

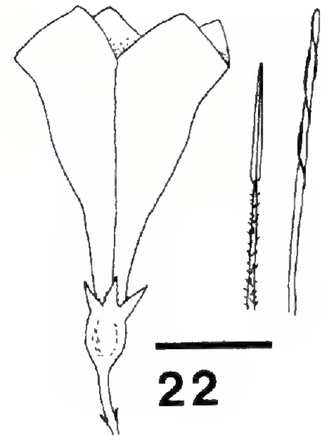
The anthers are basifixed, and dehiscence is longitudinal.

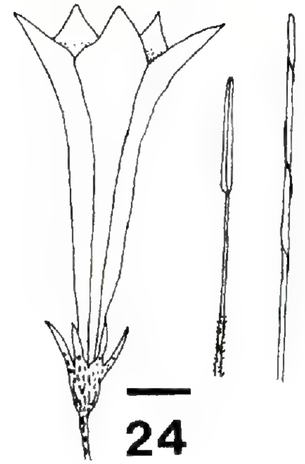
The style is the same length as the stamens, plus or minus 1–2 mm. Unlike the stamen filaments, the style is glabrous.

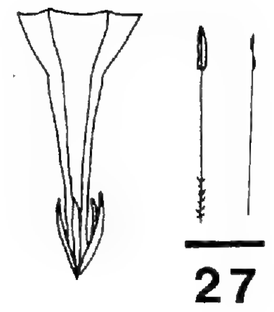
The stigmatic area consists of two (rarely three) narrow lines of papillae that begin at the apex of the style and continue down the outside for a distance of 0.2 to 6 cm. Usually these two lines are twisted several times around the style. There is no obvious correlation between length of the style and length of the stigmatic area.

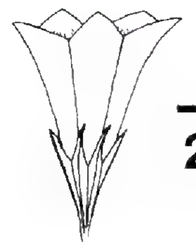
Although there is some evidence of protandry in specimens of *Hintonia*,

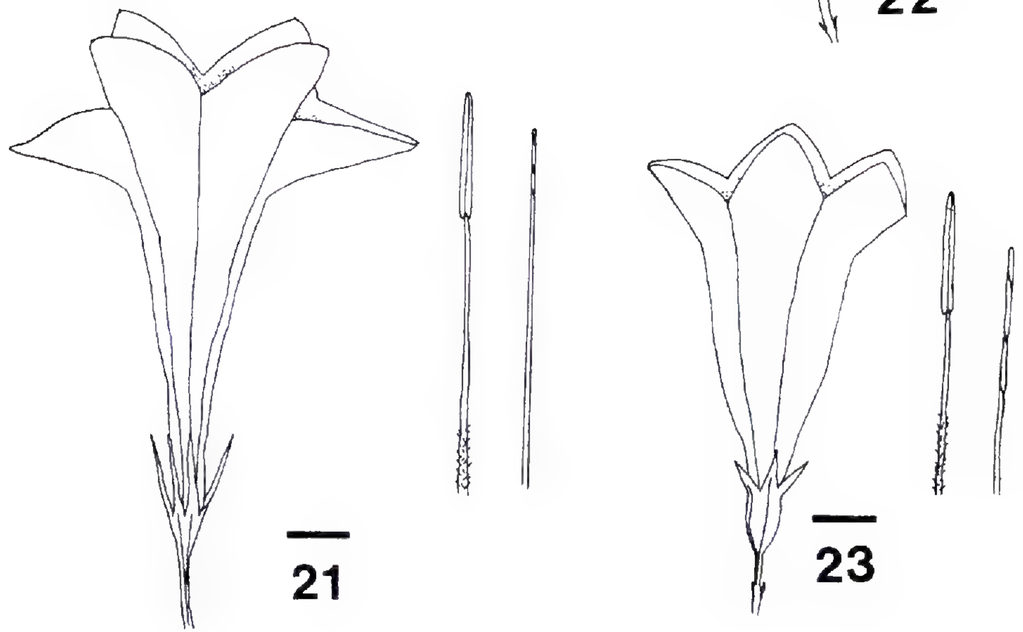


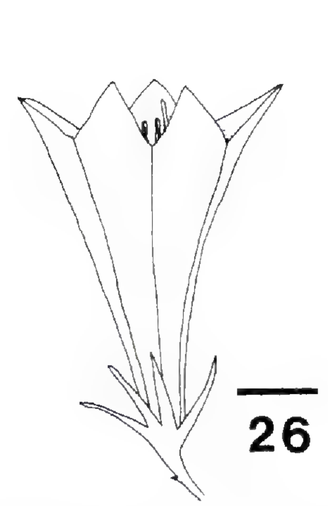


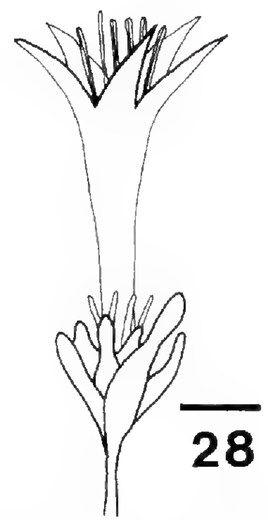








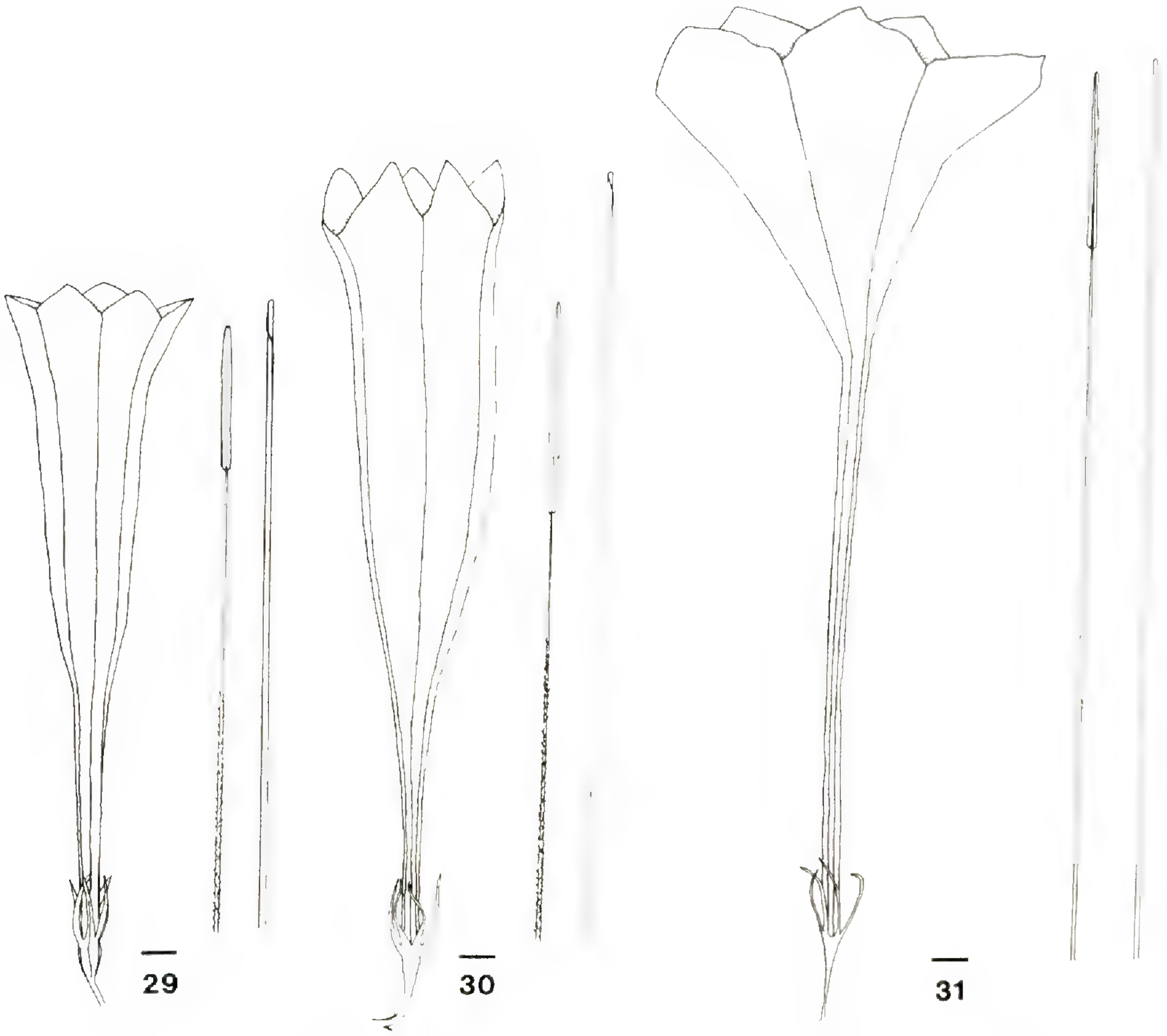




FIGURES 20–28. Flowers, stamens, and styles: 20, *Coutarea hexandra* (*Allen 796* (MO)); 21, *Hintonia latiflora* (*Gentry 7064* (DS)); 22, *Coutaportla ghiesbreghtiana*; 23, *Cigarrilla mexicana* (*Aiello 1237* (A)); 24, *Siemensia pendula*; 25, *Schmidtottia elliptica* (*Alain 915* (NY)); 26, *Schmidtottia cubensis*; 27, *Isidorea pedicellaris*; 28, *Ceuthocarpus involucratus*. Bar scales = 10 mm.

the other genera appear to produce fertile stamens and receptive stigmas simultaneously.

COLLETERS. The term "colleters" (from the Greek, meaning glued or fastened together) was first used by Hanstein (1868) to refer to secretory glands or trichomes found on bud scales, leaves, or stipules. Colleters



FIGURES 29–31. Flowers, stamens, and styles: 29, *Cubanola domingensis*; 30, *Thogsennia lindeniana*; 31, *Osa pulchra* (*Burger 7320* (F)). Bar scales = 10 mm.

range in length from 0.2 mm. to 2 mm., and their shape varies from linear-lanceolate to ovate-lanceolate. Their structure is distinctive and consists of a central core of elongate cells with a layer of even more elongate cells perpendicular to and radiating from it.

While colleters were described as early as 1849 by Weddell, we still know very little about their distribution and structural variation, and practically nothing about their secretory products or their function.

Various terms have been applied to colleters. Weddell (1849), Lawson (1854), Mitra (1948), and Jayaweera (1963) referred to them as "glands," or "glandular hairs." Solereder (1899) and Metcalfe and Chalk (1950) called them "Drüsenzotte" (shaggy glands). Foster (1949), Esau (1965),

Lersten (1974, 1975), and Lersten and Curtis (1974) use Hanstein's term "colleters."

Jayaweera (1963a, 1963b, 1964, 1965) used colleter number and arrangement as a taxonomic tool in his studies of *Mussaenda*. He found colleters on the calyx as well as on the stipules.

During the present study also, colleters were found on both calyx and stipules (FIGURES 33–44; TABLE 3). In order to examine stipules for colleters, an entire apical bud must be destroyed. Because very little material was available for study, stipules were dissected only in those taxa (*Coutaportla*, *Cigarrilla*, and *Portlandia*) where my own field collections were made, and in *Siemensia pendula*, where abundant herbarium material was available.

All five species of *Portlandia* bear several rows of colleters along the base of the adaxial surface of the stipules (FIGURE 41). There are no apparent differences in number or arrangement of colleters among the five species.

In *Cigarrilla* and *Siemensia* the colleters are arranged in two groups of about fifteen each and are located in the lower corners of the stipules (FIGURES 43, 44). *Cigarrilla* has a few scattered colleters toward the center of each stipule as well.

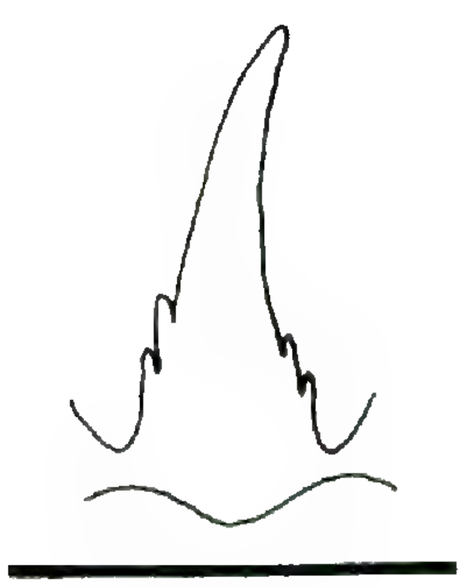
In *Coutaportla* the entire inner surface of the stipule is covered with colleters (FIGURE 42). They can be seen from the outside of the stipule as a fringe along its edges.

Calyx colleters are found in *Cigarrilla*, *Coutarea*, *Cubanola*, *Osa*, and *Thogsennia*. They are also present in *Portlandia grandiflora* and *P. harrisii*, but not in *P. coccinea*, *P. microsepala*, or *P. platantha*. Among the four species of *Isidorea* examined, they were found on *I. leonardii* and *I. pedicellaris*, but not on *I. leptantha* or *I. pungens* (FIGURES 33–40). Their structure is the same as that of the more widely known stipular colleters. Calyx colleters are absent from *Ceuthocarpus*, *Hintonia*, *Schmidtottia*, *Siemensia*, and *Coutaportla*. The calyx lobes of *Coutaportla* have red-tipped glands along the edges (FIGURE 32).

There is much variation as to number and arrangement of calyx colleters. In *Isidorea* there are two per sepal, while *Portlandia grandiflora* has four, and *Cigarrilla* has six. *Portlandia harrisii* has a continuous ring of colleters within the base of the calyx. In *Coutarea* the colleters are arranged in groups between the sepals. *Osa*, *Cubanola*, and *Thogsennia* have more abundant colleters, and these extend up onto the inner face of each sepal.

POLLEN

Pollen in the Rubiaceae is rather diverse. According to Erdtman (1952), 3-polycolpate, 2- to 4-colporate, 3-porate, polyforate, and nonaperturate types occur in the family. As part of the present study, pollen of the major genera of the tribe Condamineeae was examined, as was that of a



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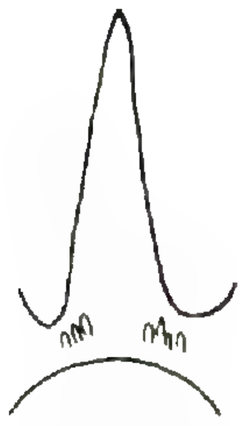

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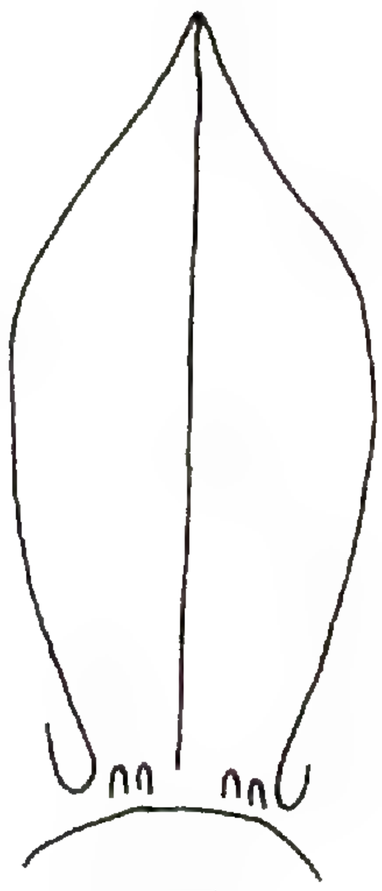

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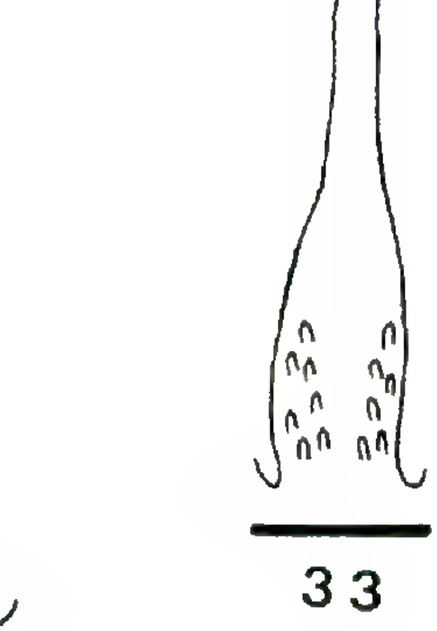

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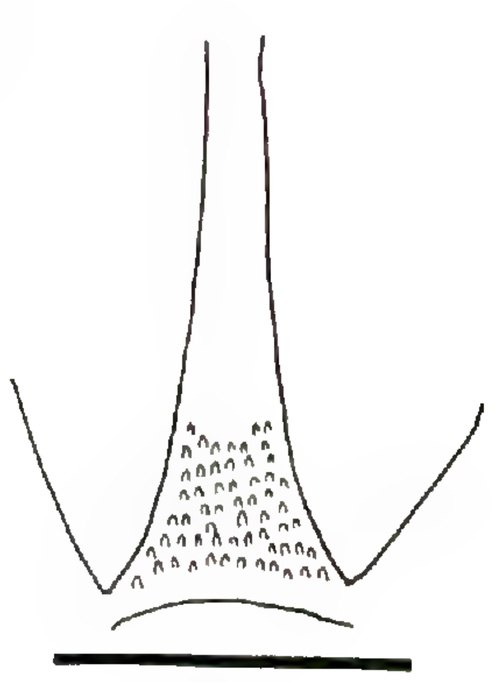

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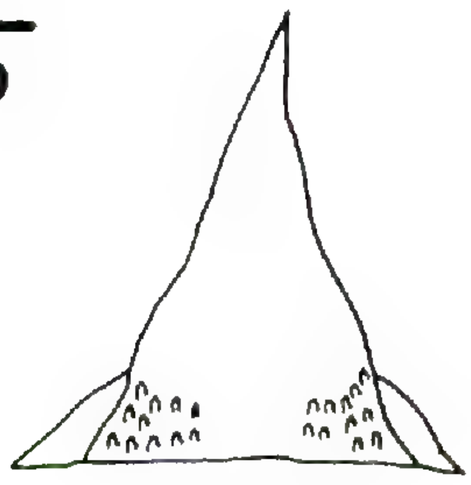

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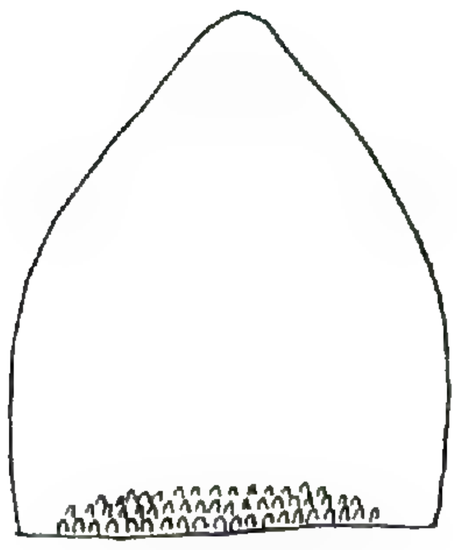

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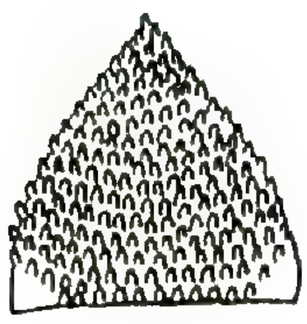

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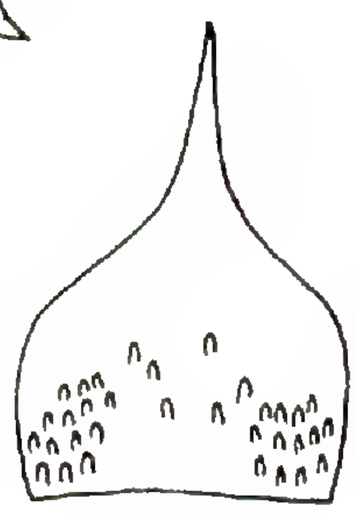

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FIGURES 32–44. *32*, glands on edge of calyx lobe of *Coutaportla ghiesbreghtiana*. Bar scale = 3 mm. 33–40, colleters on calyx lobes: *33*, *Thogsennia lindeniana*; 34, *Isidorea pedicellaris*; 35, *Cigarrilla mexicana* (*Aiello 1237* (A)); 36, *Portlandia grandiflora*; 37, *Portlandia harrisii* (*Aiello 1306* (A)); 38, *Coutarea hexandra* (*Allen 796* (NY)); 39, *Cubanola domingensis*; 40, *Osa pulchra*. Bar

number of genera assigned to the tribes Cinchoneae and Rondeletieae, for comparison with pollen of *Portlandia*.

Pollen was removed from herbarium specimens and placed on aluminum stubs by means of double-stick Scotch tape. The stubs were then coated, first with carbon in two one-minute steps, and then with gold-palladium in two 1.5-minute steps, using a Technics Hummer II sputter coater. The specimens were examined with an AMR model 1000a scanning electron microscope in the secondary electron mode using accelerating voltages up to 20 KV. Polaroid type 55 P/N 4″ × 5″ film was used to record scanning electron micrographs. The micrographs were made at the Museum of Comparative Zoology, Harvard University, scanning electron microscope facility (funded under NSF Grant No. BMS-7412494).

Acetolyzed pollen of seven genera was examined under the compound light microscope. Measurements are equatorial (width) followed by polar (length).

All of the pollen studied was tricolporate, and fell into one of three main sculpture types.

Type I (FIGURES 45, 46). The pollen of *Bikkia* (14 μm. × 13 μm.), *Cigarrilla* (17 μm. × 25 μm.), *Coutaportla* (20 μm. × 20 μm.), *Coutarea* (20 μm. × 19 μm.), *Cubanola* (26 μm. × 31 μm.), *Exostema* (28 μm. × 22 μm.), *Hintonia* (16 μm. × 24 μm.), *Isidorea* (12 μm. × 23 μm.), *Osa* (26 μm. × 31 μm.), *Portlandia* (21 μm. × 24 μm.), *Schmidtottia* (29 μm. × 27 μm.), *Siemensia* (17 μm. × 17 μm.), *Thogsennia* (16 μm. × 20 μm.), and the doubtfully placed *Portlandia guatemalensis* (17 μm. × 16 μm.) is fairly uniform except for size. It is tricolporate, spherical to prolate, and diffusely foveolate, and bears echinate to bluntly echinate processes. Interpretation of SEM pictures is sometimes difficult due to swelling of the grains.

Type II (FIGURES 47, 48). In general, this type of pollen is tricolporate and prolate to spherical; the surface is foveolate and lacking in tectal processes. *Macrocnemum* (11 μm. × 19 μm.) is spherical to prolate, with large, widely scattered foveae. *Rondeletia intermixta* (8 μm. × 8 μm.) and *R. pachyphylla* (12 μm. × 14 μm.) are prolate and diffusely foveolate. *Rustia formosa* (15 μm. × 26 μm.) and *Cinchona pubescens* (15 μm. × 17 μm.) are densely foveolate. *Tresanthera* (18 μm. × 17 μm.) is spherical and rugulate, with foveae in the depressions.

Type III (FIGURES 49, 50). This type of pollen is tricolporate, prolate to spherical, and foveolate-reticulate to reticulate-foveolate. *Condaminea* (19 μm. × 24 μm.) and *Chimarrhis cymosa* (14 μm. × 16 μm.) are foveolate to foveolate-reticulate. *Chimarrhis latifolia* (14 μm. × 17 μm.) and *C. parvifolia* (12 μm. × 13 μm.) are reticulate. *Bathysa* (9 μm. × 16

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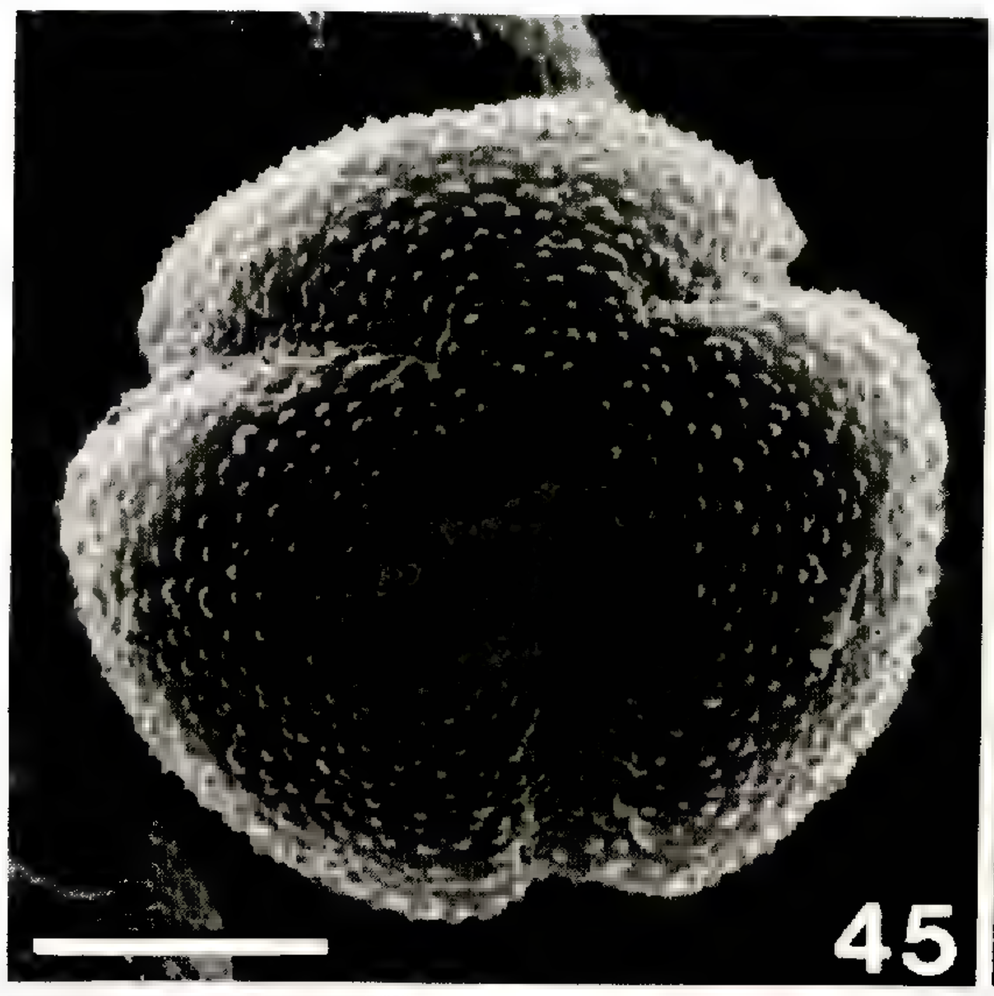
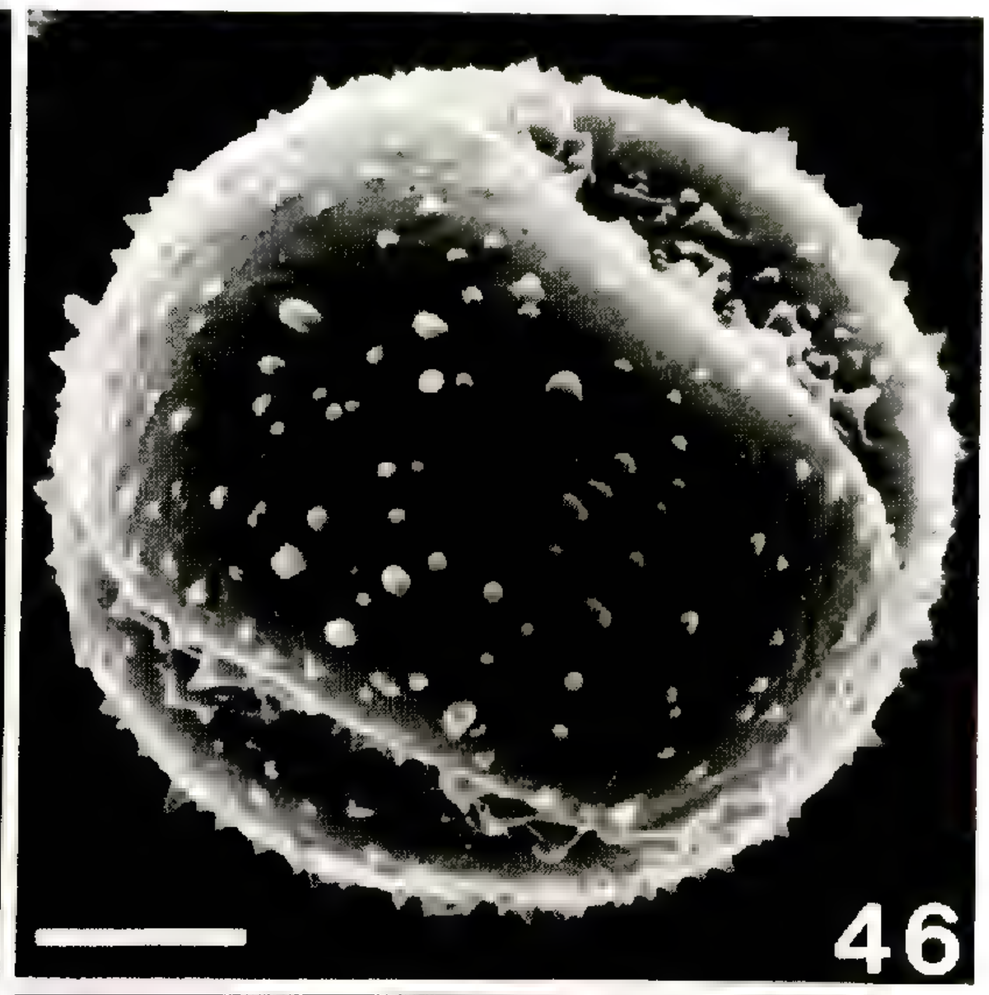
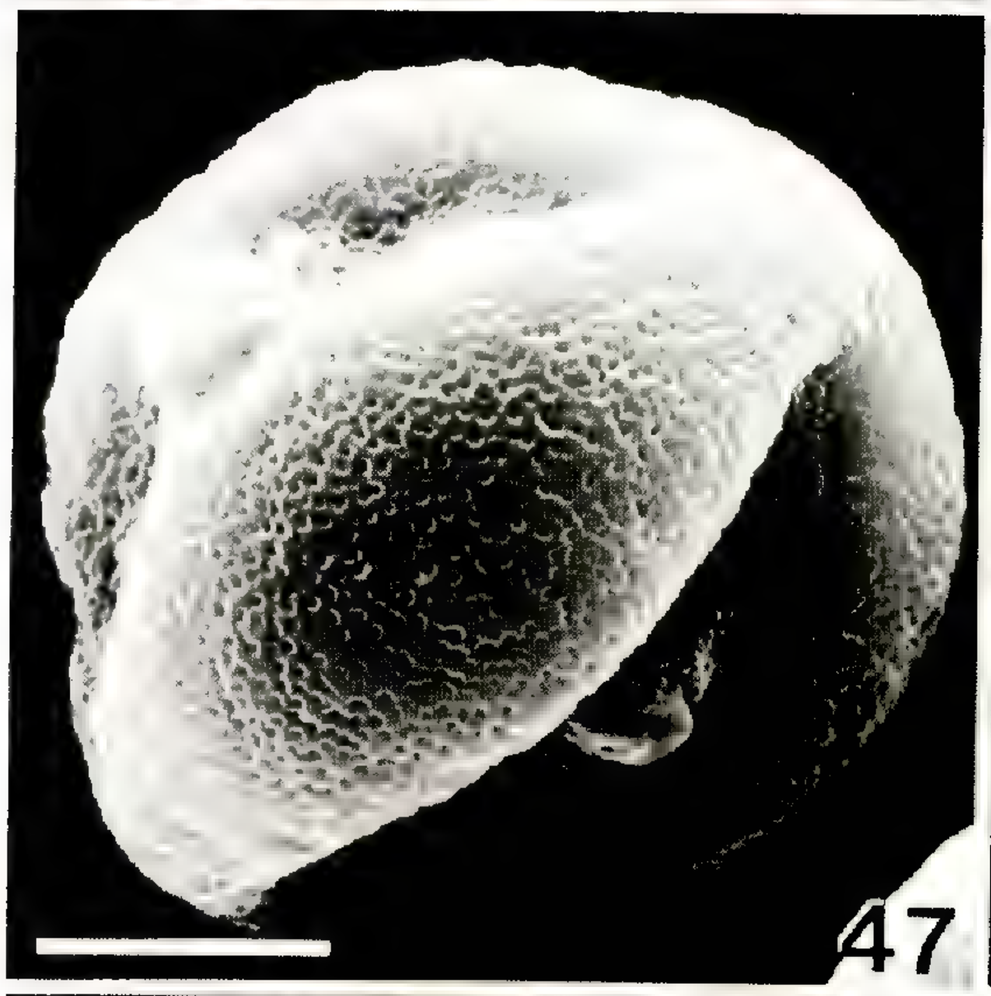
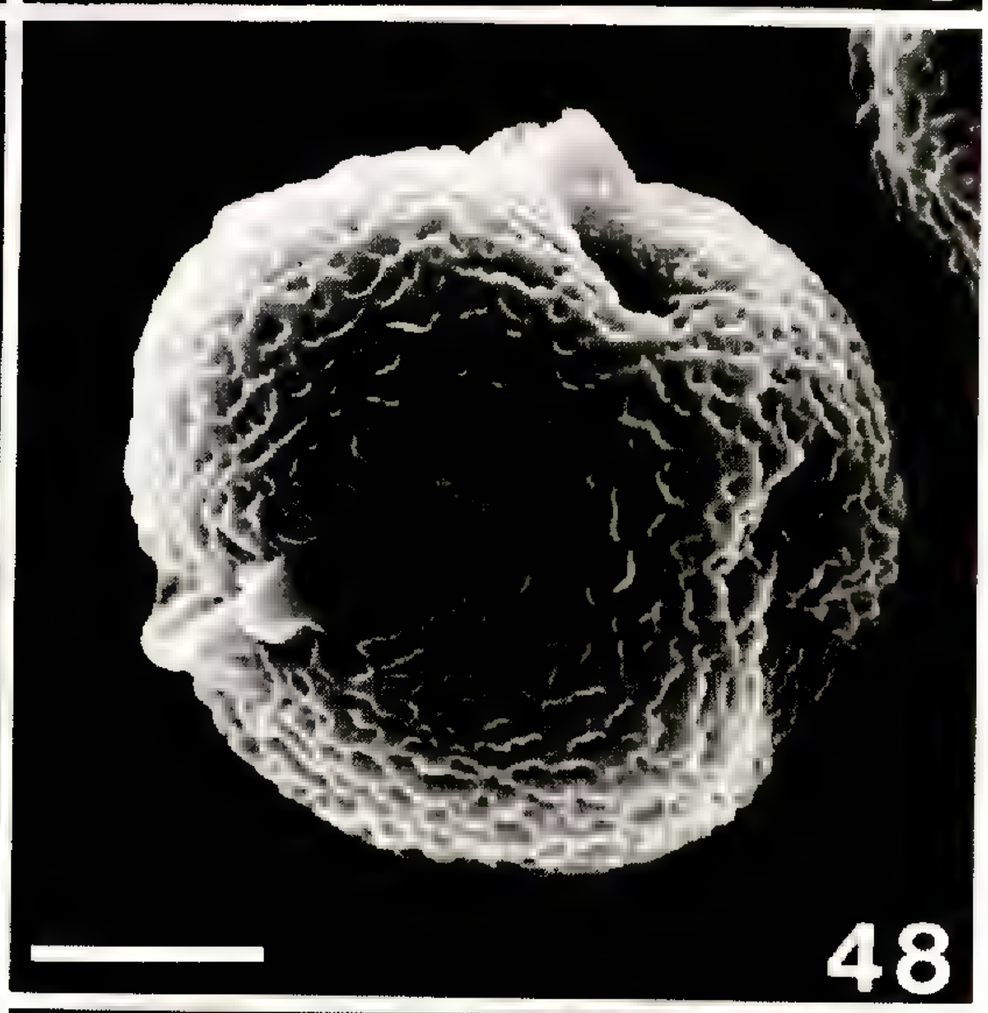
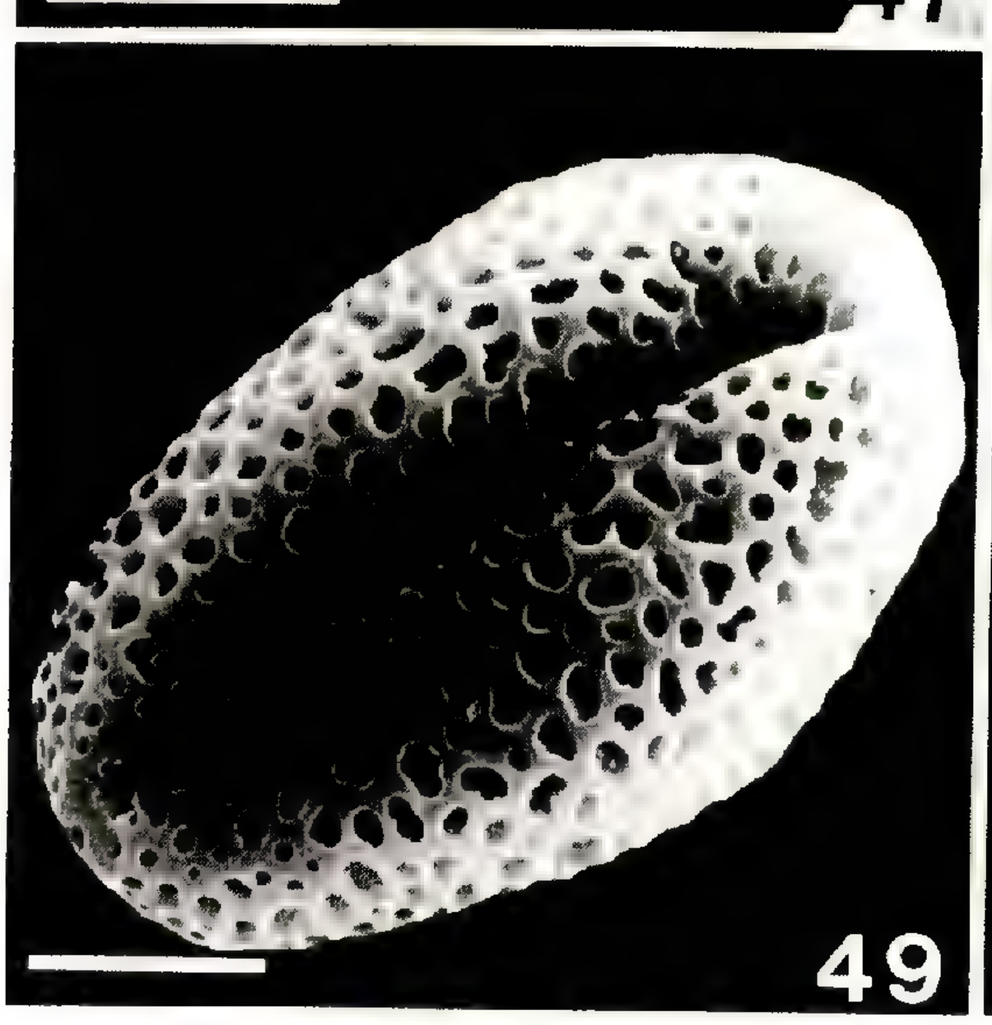
scales = 3 mm. 41–44, colleters on stipules: 41, *Portlandia harrisii*; 42, *Coutaportla ghiesbreghtiana*; 43, *Siemensia pendula*; 44, *Cigarrilla mexicana*. Bar scales = 2 mm.

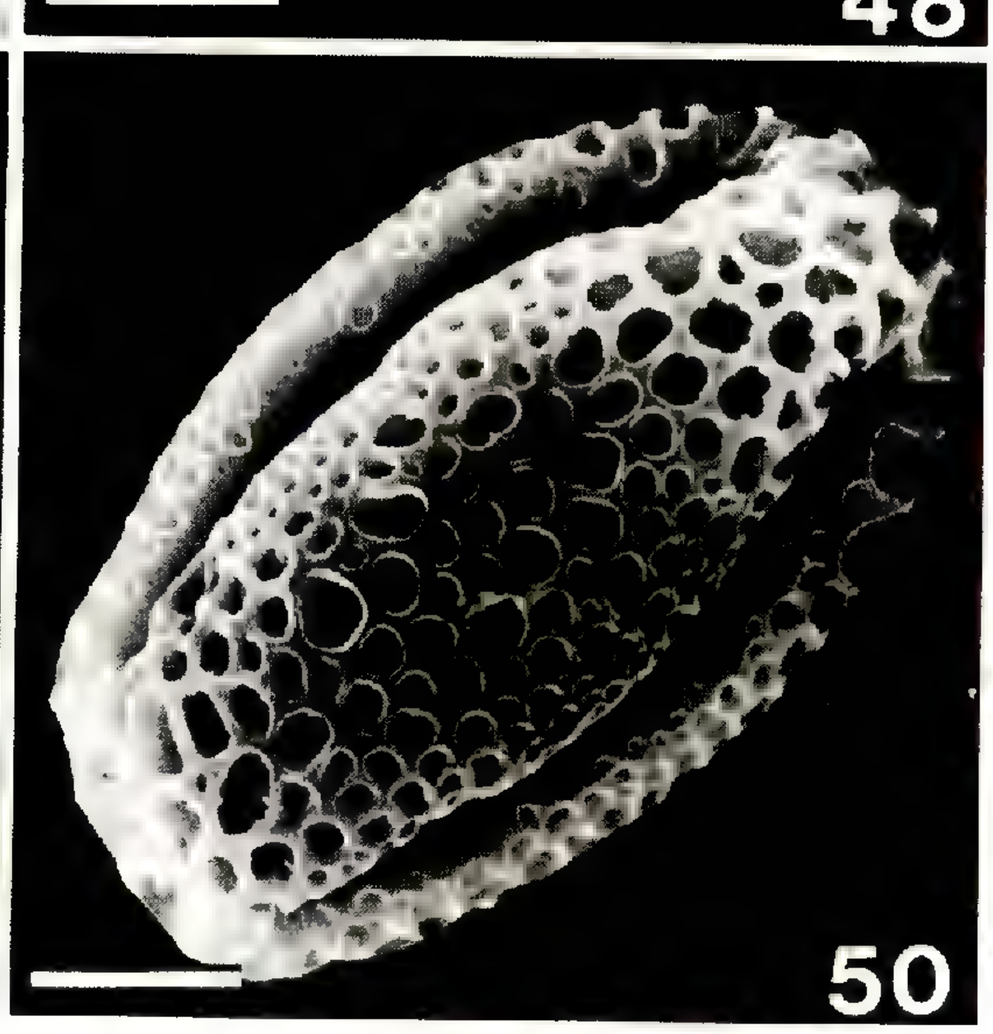












FIGURES 45–50. Pollen: 45, *Isidorea brachycarpa* (*Carabia 3809* (GH)); 46, *Portlandia microsepala* (*Howard 14598* (IJ)); 47, *Cinchona pubescens* (*Hodge 6534* (GH)); 48, *Tresanthera pauciflora* (*Webster 9805* (A)); 49, *Pinckneya pubens* (*Gillespie 5091* (A)); 50, *Rustia occidentalis* (*Svenson 331* (GH)). Bar scales = 5 μm.

μm.) and *Lindenia* (13 μm. × 14 μm.) are reticulate to reticulate-foveolate. *Calderonia* (17 μm. × 26 μm.), *Picardaea* (12 μm. × 22 μm.), *Pinckneya* (14 μm. × 25 μm.), *Pogonopus* (12 μm. × 15 μm.), and *Rustia occidentalis* (14 μm. × 22 μm.) are reticulate.

As TABLE 4 shows, the Rondeletieae are not represented in pollen type

TABLE 4. **Distribution of pollen and wood types among genera surveyed.**

POLLEN TYPE	GENUS	TRIBE*	KOEK-NOORMAN WOOD TYPE†
I	*Bikkia*	Co	II
I	*Ceuthocarpus*	Co	
I	*Coutaportla*	Ci	
I	*Coutarea*	Ci	
I	*Exostema*	Ci	II
I	*Hintonia*	Ci	
I	*Isidorea*	Co	
I	*Portlandia*	Co	II
I	*Schmidtottia*	Co	
I	*Siemensia*	Co	
I	*Thogsennia*	Co	
II	*Cinchona*	Ci	I
II	*Ladenbergia*	Ci	II
II	*Macrocnemum*	Ci	I
II	*Rondeletia*	R	II
II	*Rustia formosa*	Co	I
II	*Tresanthera*	Co	
III	*Bathysa*	R	I
III	*Calderonia*	Co	
III	*Chimarrhis*	Co	I
III	*Condaminea*	Co	I
III	*Lindenia*	R	II
III	*Picardaea*	Co	
III	*Pinckneya*	Co	I
III	*Pogonopus*	Co	I
III	*Rustia occidentalis*	Co	I

* Co = Condamineeae, Ci = Cinchoneae, R = Rondeletieae.
† Where known.

I, and the Cinchoneae are absent from type III, while all three tribes have genera with type II pollen. The genus *Rustia* displays both types II and III. In addition, these two types appear to grade into one another, especially when they are compared with pollen of *Macrocnemum*. Type II may simply be immature type III pollen.

There is some correlation between pollen types and the wood types of Koek-Noorman and Hogeweg (1974). Future work will likely result in revision of these three tribes, since many genera appear to be misplaced. *Siemensia*, for example, probably belongs to the Hedyotideae rather than the Condamineeae. However, the possibility also remains that there is

some ecological reason for the pollen differences. In general, the genera with type I pollen tend to have much larger, showier flowers than do the other genera. Perhaps these larger-flowered genera have either similar pollinators or different pollinators with similar habits. In the case of *Portlandia*, for example, the white-flowered species are probably pollinated by moths, and the red-flowered species by hummingbirds. Both of these pollinators are fairly large, and both hover while feeding at the flowers. Practically nothing is known on the general subject of pollen-type/pollinator relationships.

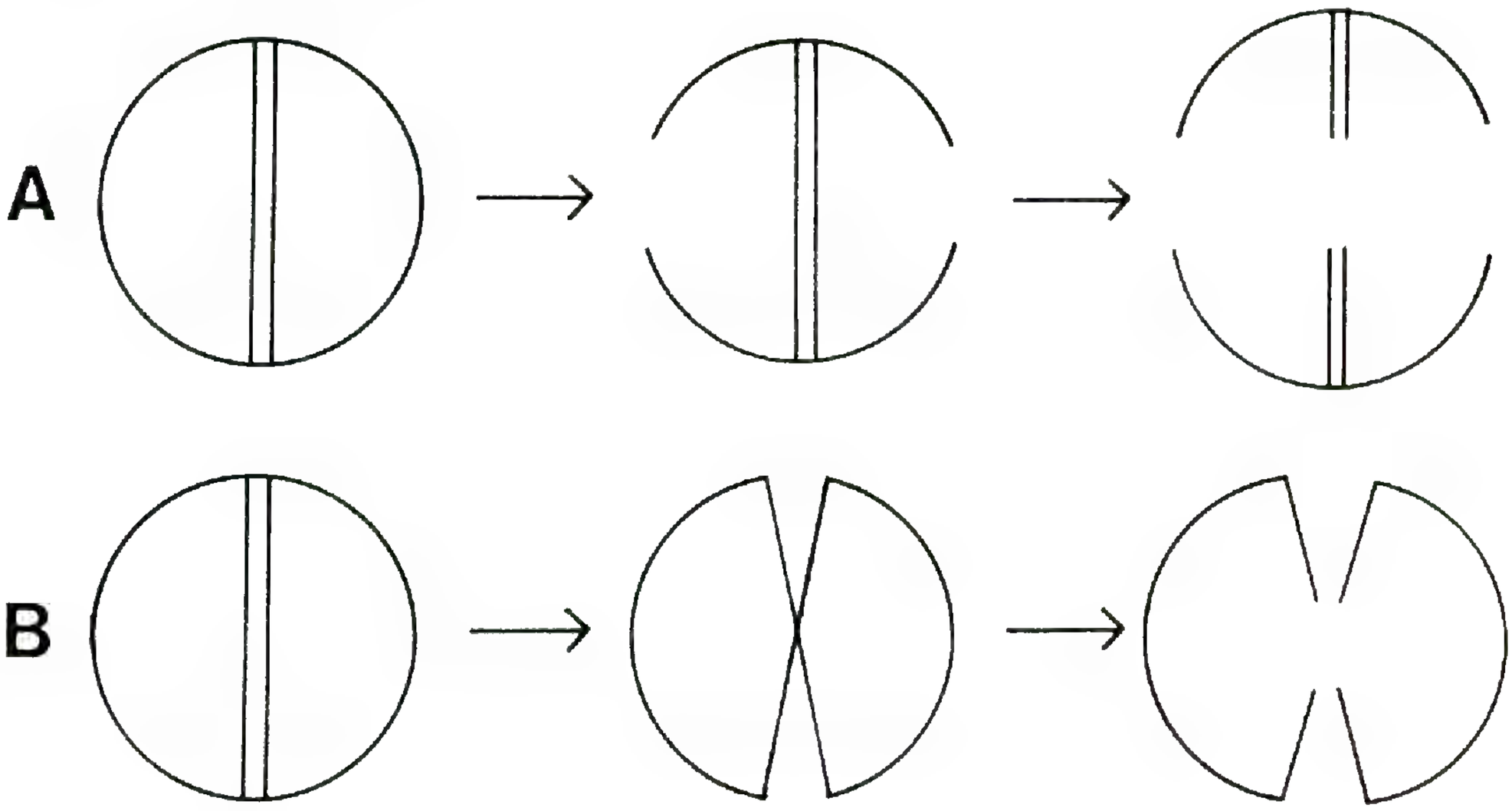


FIGURE 51. Diagrammatic cross sections of capsules showing double-walled septum: A, loculicidal splitting of capsule followed by septal splitting; B, septicidal splitting of capsule wall plus septal separation followed by septal splitting.

FRUITS

Fruit and seed characters are very important to the understanding of the Rubiaceae, yet they have often been either underrated or neglected altogether. For example, although Baillon (1879) gave an excellent description of the fruit of what we now know as *Coutaportla*, he did not recognize the plant as a distinct genus but rather as a section of *Portlandia*. It remained for Urban (1923) to make a generic separation based on a number of characters including placental shape and seed attachment. Bullock (1935), in separating *Hintonia* from *Portlandia* and *Coutarea*, considered seeds winged vs. unwinged, and capsules septicidal vs. loculicidal as well as flattened vs. unflattened, and decided that, in spite of the fact that *Hintonia* has winged seeds, it is closer to *Portlandia* than to *Coutarea*. He also stated that the seeds of *Hintonia* are descending, while those of *Coutarea* are ascending, but he made no mention of seed attachment in *Portlandia*. When Urban (1923) separated *Siemensia* from *Portlandia*, he did so on the basis of leaf anatomy, with no discussion of differences in fruits or seeds.

The following discussion is an attempt to describe the diversity of fruit forms present among the taxa at one time included in the genus *Portlandia*.

Capsule size and shape are quite variable within, as well as among, genera and species. TABLE 5 shows length × width index and length of

TABLE 5. **Fruit size for Portlandia and associated taxa.**

LENGTH × WIDTH INDEX	LENGTH (cm.)	TAXON
882	4.2	*Cubanola domingensis*
667	4.2	*Thogsennia lindeniana*
590	3.0	*Cubanola daphnoides*
411	2.6	*Portlandia grandiflora*
406	2.8	*Coutarea* spp.
378	2.5	*Hintonia latiflora*
352	3.2	*Osa pulchra*
320	2.0	*Portlandia harrisii*
205	1.6	*Portlandia platantha*
192	1.6	*Hintonia standleyana*
178	1.6	*Cigarrilla mexicana*
173	1.8	*Hintonia octomera*
170	1.5	*Portlandia coccinea*
141	1.5	*Isidorea polyneura*
132	1.2	*Isidorea pungens*
124	1.6	*Isidorea leptantha*
110	1.1	*Isidorea pedicellaris*
107	1.1	*Ceuthocarpus involucratus*
88	1.1	*Isidorea brachyantha*
84	1.2	*Isidorea oblanceolata*
84	1.2	*Schmidtottia uliginosa*
80	1.2	*Schmidtottia cubensis*
72	0.9	*Schmidtottia elliptica*
66	1.1	*Isidorea leonis*
66	1.0	*Hintonia lumaeana*
60	1.0	*Schmidtottia marmorata*
56	0.9	*Siemensia pendula*
56	0.8	*Coutaportla ghiesbreghtiana*
54	0.9	*Schmidtottia sessilifolia*
45	0.9	*Schmidtottia nitens*
40	0.8	*Schmidtottia parvifolia*
35	0.7	*Isidorea tetramera*
30	0.6	*Isidorea elliptica*
25	0.5	*Schmidtottia monantha*
20	0.5	*Isidorea leonardii*

average capsules for the taxa under study. The largest capsules are found in *Thogsennia lindeniana* and *Cubanola domingensis*, while those of *Osa pulchra*, *Cubanola daphnoides*, *Coutarea*, *Portlandia grandiflora*,

and *Hintonia latiflora* are considered intermediate in size. Thus the two species of *Cubanola* are closer in capsule size to unrelated taxa than to each other. The smallest capsules are found in the smooth-leaved species of *Isidorea* (*I. elliptica, I. leonardii,* and *I. tetramera*) and in *Schmidtottia monantha.* The veiny-leaved species of *Isidorea* are in the same general size range as *Siemensia, Coutaportla, Schmidtottia, Ceuthocarpus,* and *Cigarrilla,* which are all unrelated to one another. The species of *Hintonia* and *Portlandia* have very similar capsule size ranges. *Portlandia* and *Isidorea,* which are closely related genera, have no overlap in capsule size.

As can be seen from TABLE 6, capsule shape is also extremely variable.

TABLE 6. **Fruit shape for Portlandia and associated genera.**

GENUS	SHAPE(S)
Ceuthocarpus	ellipsoid to subglobose
Cigarrilla	obovoid or oblong-ellipsoid
Coutaportla	compressed; widely ovate to circular
Coutarea	compressed, obovate
Cubanola	ellipsoid, or obovoid with apex truncate
Hintonia	ellipsoid to obovoid
Isidorea	ellipsoid-oblong to obovoid or subglobose
Osa	obovoid
Portlandia	ellipsoid to widely obovoid or globose, rarely ovoid
Schmidtottia	obovoid or ellipsoid-oblong; apex truncate
Siemensia	ellipsoid to obovoid; apex truncate
Thogsennia	ellipsoid to oblong or somewhat obovoid

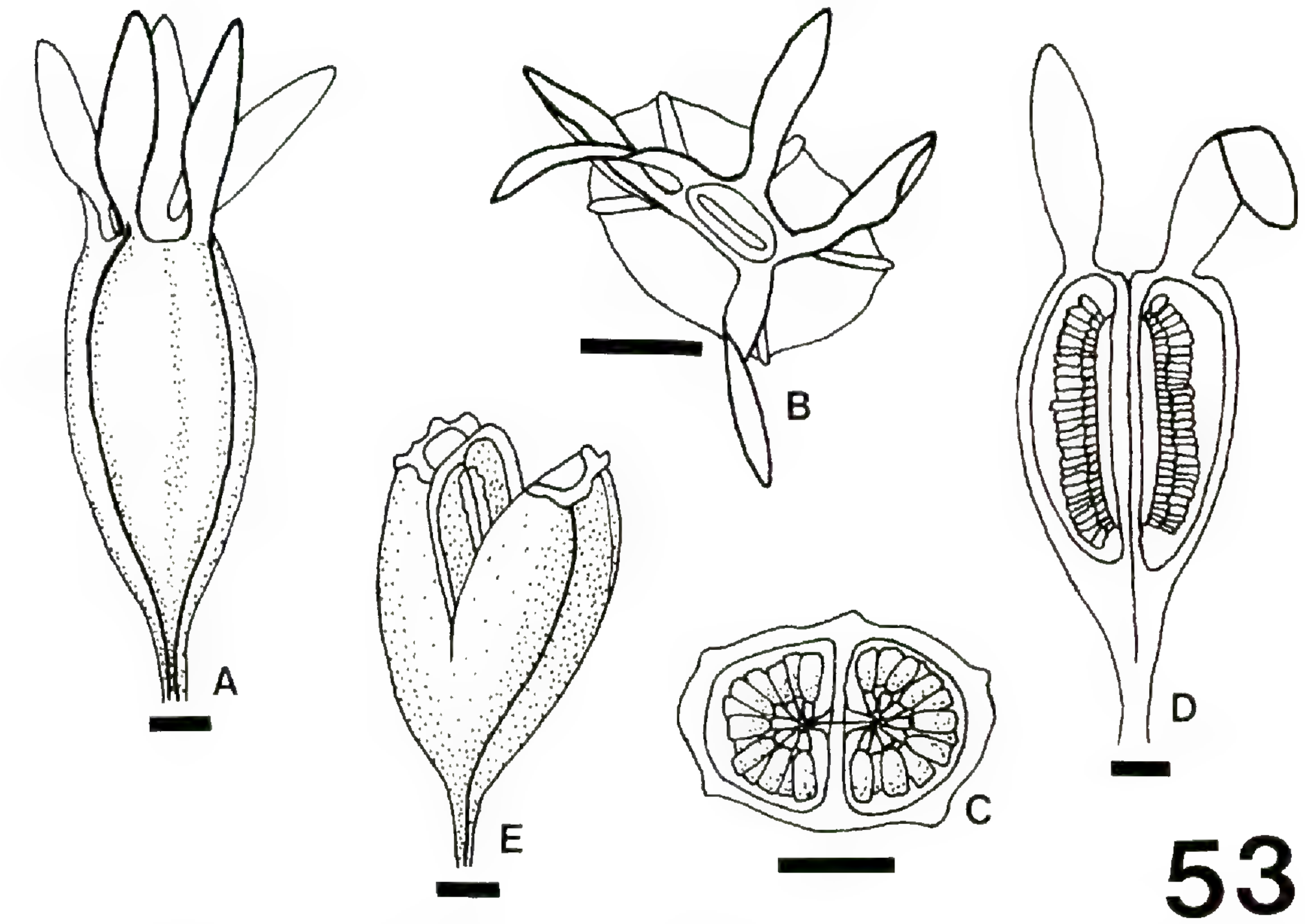
The only really distinctive capsules are those of *Coutaportla* and *Coutarea,* which are highly compressed; they can, however, be distinguished from one another on the basis of size and shape.

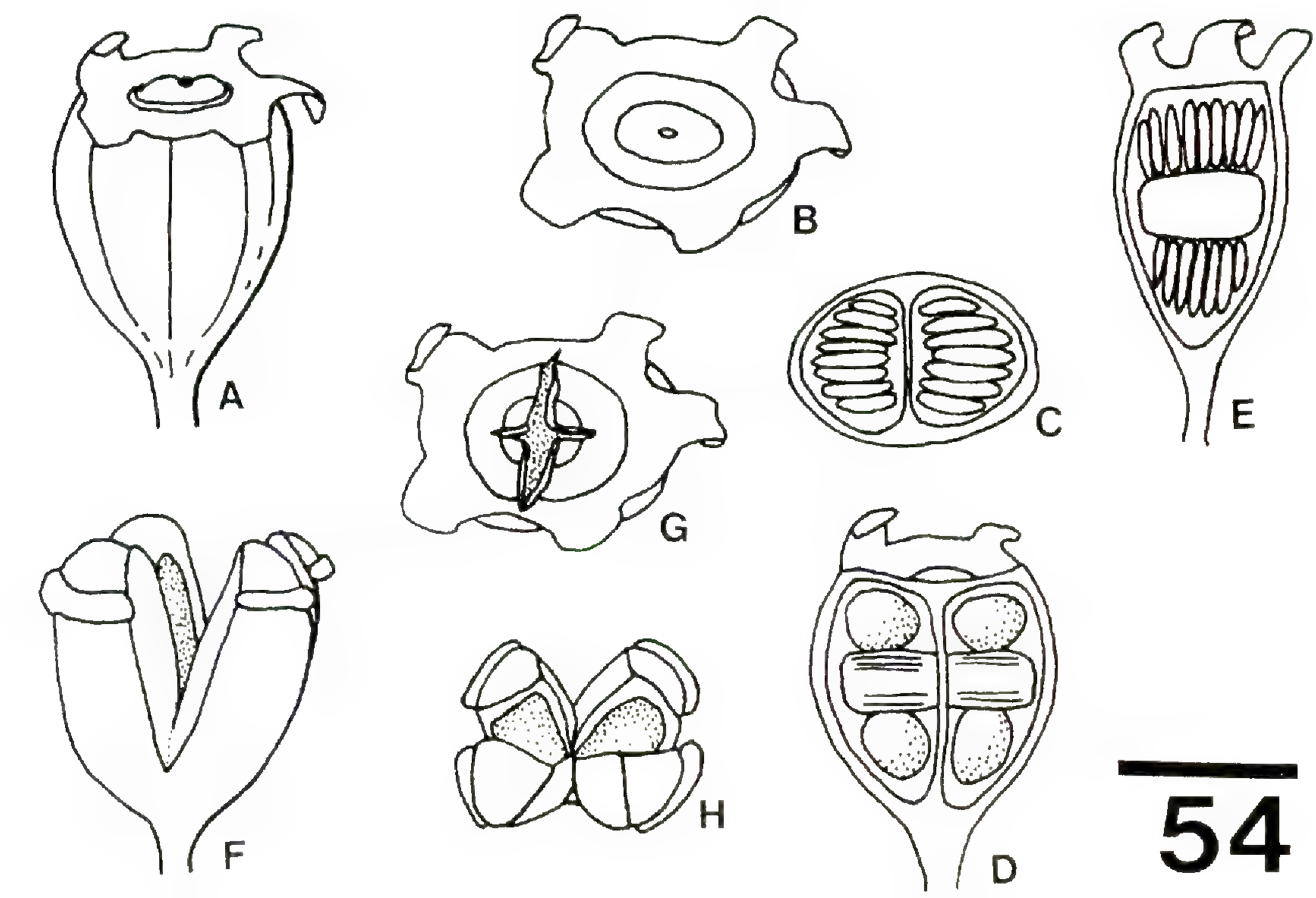
Although *Isidorea* species seem to fall into two distinct groups based on capsule size and leaf texture, fruit size and shape appear to have little taxonomic meaning among the genera under study beyond their use as aids in the identification of certain taxa.

There are three possible processes involved in the capsule dehiscence of *Portlandia* and associated genera (with the exception of *Thogsennia,* which is indehiscent). In some genera all three of these processes occur, while in others only two are observed. The three processes are: 1) loculicidal splitting of the capsule wall, starting at the top and continuing part or all of the way to the base; 2) septicidal splitting of the capsule wall, including separation of the double wall of the septum, again starting at the top and continuing part or all of the way to the bottom; and 3) splitting of the septum walls along a mid-longitudinal line — this splitting may begin at the top and continue part or all of the way down, or may begin at the midpoint of the septum and continue in both directions.

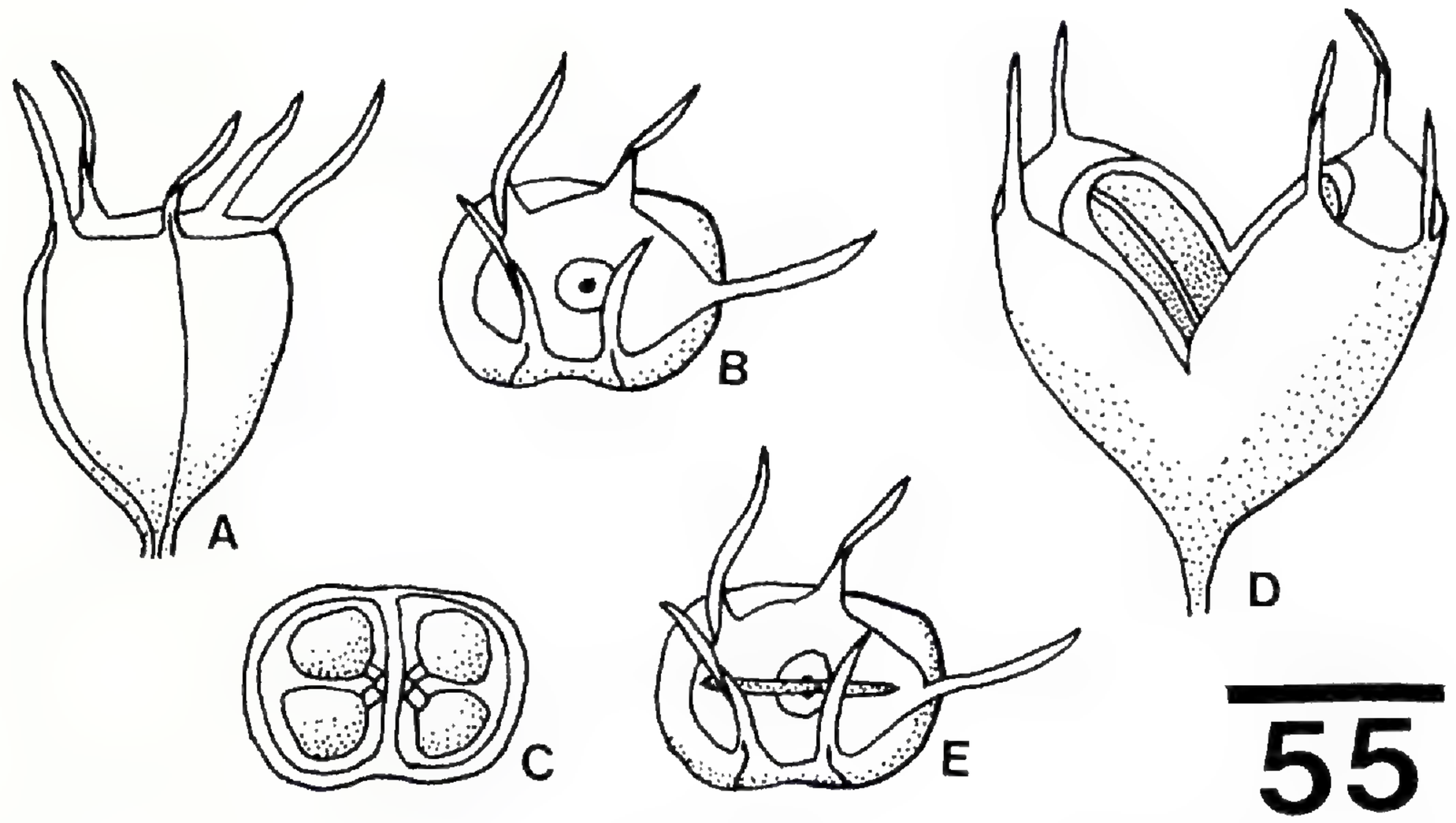
The distinction between septal "separation" (part of process 2) and septal "splitting" (process 3) is important, and the two should not be

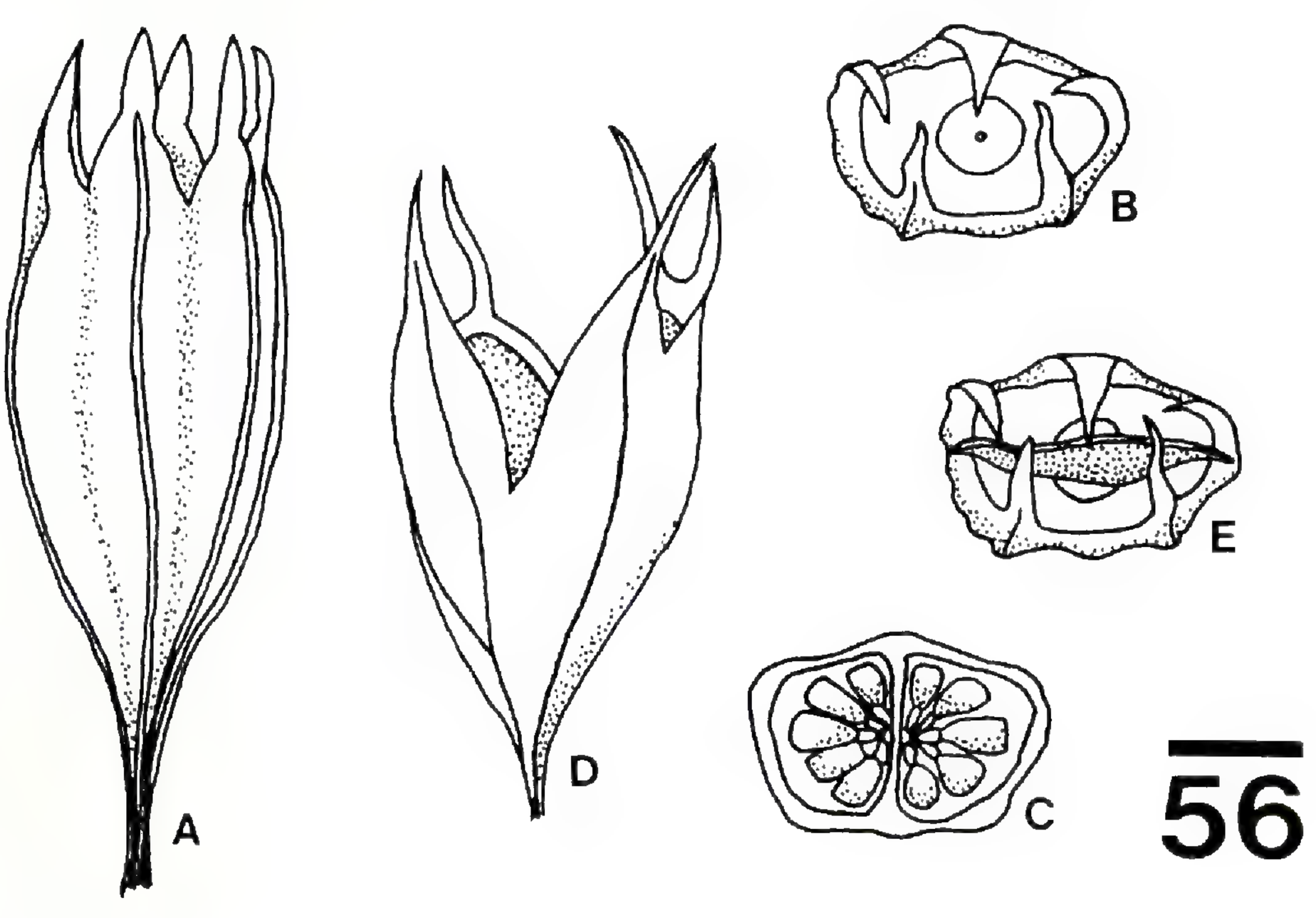
FIGURE 52. Placental shape and seed attachment and orientation in *Portlandia* and associated genera.





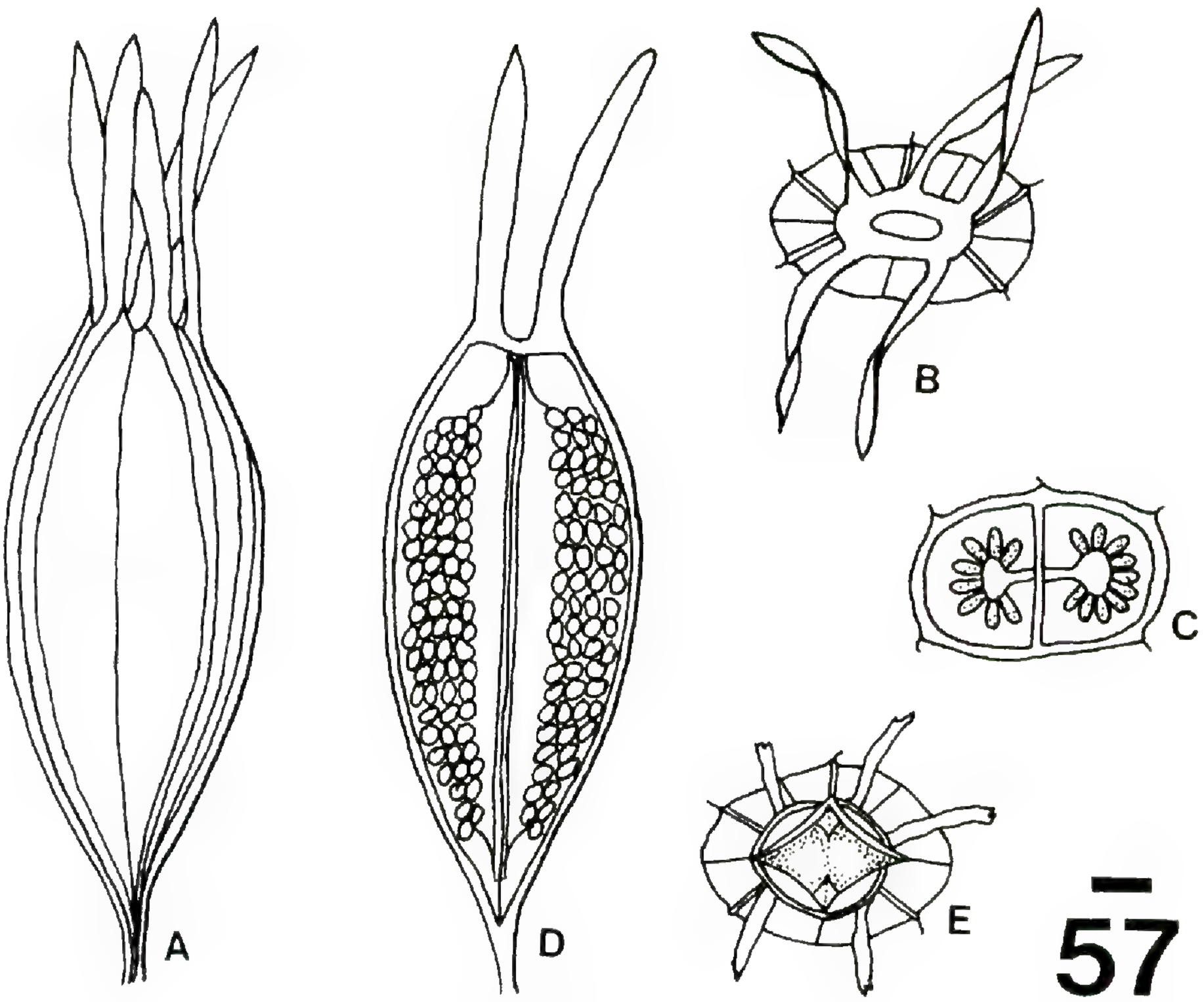
FIGURES 53, 54. Capsules. 53, *Portlandia grandiflora* (*Proctor 16657* (IJ)): A, side view; B, top view; C, cross section, septum, placentae, seeds with persistent funicles shown; D, side view, wall removed to show septum, placentae, horizontal seeds with persistent funicles; E, side view, indicating loculicidal dehiscence, septal splitting. 54, *Schmidtottia elliptica*: A, side view; B, top view; C, cross section below middle, to show septum, seeds; D, side view, wall perpendicular to septum removed, septum, placentae (center), and seeds shown;

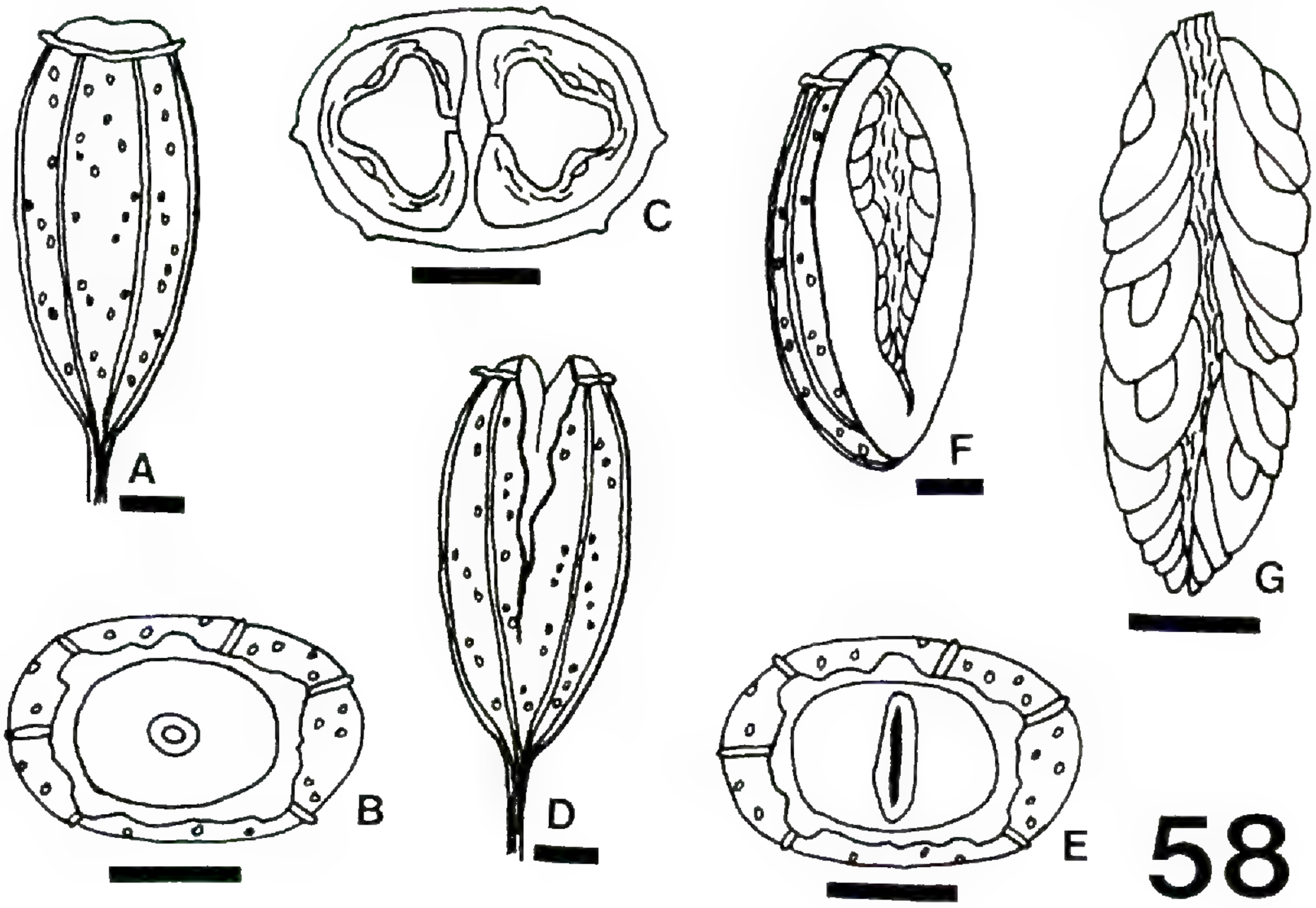




E, side view, wall parallel to septum removed to show placenta, seeds; F, side view, indicating method of dehiscence (more septicidal than loculicidal); G, top view, to show early dehiscence (more septicidal than loculicidal); H, top view, to show late dehiscence (loculicidal and septicidal). Bar scales = 5 mm.

FIGURES 55, 56. Capsules. 55, *Isidorea leonardii*: A, side view; B, top view; C, cross section through middle, septum, small placentae, horizontal seeds with persistent funicles shown; D, side view, indicating method of dehiscence (strongly loculicidal); E, top view, to show early loculicidal dehiscence. 56, *Isidorea polyneura*: A, side view; B, top view; C, cross section, septum, small placentae, horizontal seeds with persistent funicles shown; D, side view, indicating method of dehiscence (strongly loculicidal); E, top view, to show early loculicidal dehiscence. Bar scales = 5 mm.





FIGURES 57, 58. 57, capsule of *Cubanola domingensis*: A, side view; B, top view; C, cross section through middle, showing septum, stalked placentae, horizontal seeds; D, side view, wall removed, showing septum, horizontal seeds; E, top view, showing dehiscence (loculicidal and septicidal) limited to disc area. 58, *Hintonia latiflora*. A–F, capsule: A, side view; B, top view; C, cross section

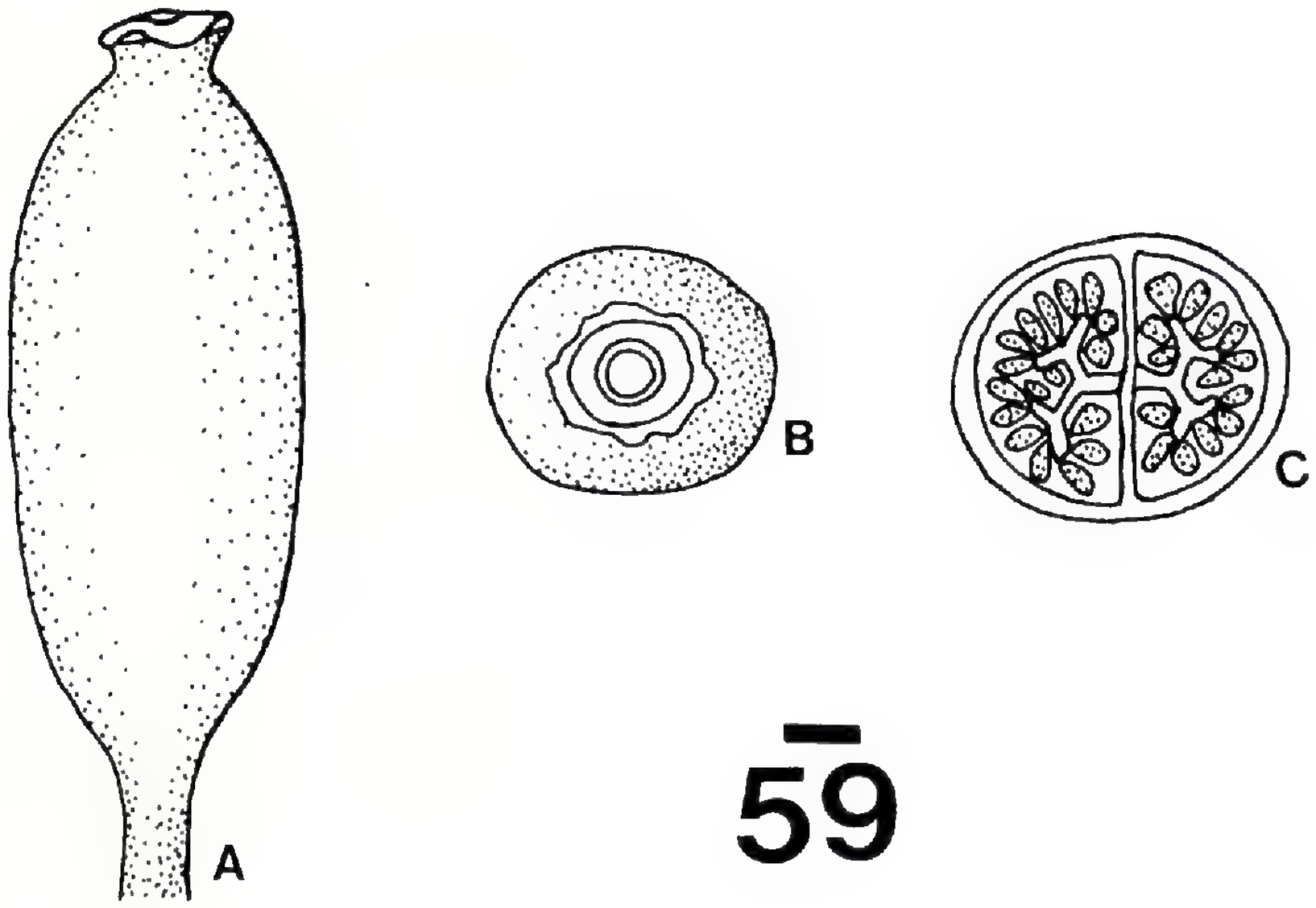


FIGURE 59. Capsule of *Thogsennia lindeniana*: A, side view; B, top view; C, cross section, septum, twice-forked placentae, and horizontal seeds shown. Bar scale = 5 mm.

confused. In the case of loculicidal dehiscence, splitting of the septum allows the capsule to spread open (FIGURE 51, A) and expose the seeds. In the case of septicidal dehiscence, the seeds cannot escape unless the septum splits (FIGURE 51, B).

Hintonia dehisces septicidally, and not at all loculicidally, resulting in the separation of the two locules. The additional splitting and slight curving of the septum allows the seeds to escape. *Osa* may have this same type of dehiscence, but the single capsule available for study had not yet opened.

Portlandia and *Isidorea* are loculicidally dehiscent with simultaneous septal splitting. The resulting two valves of the capsule spread away from each other, exposing the seeds.

The remaining genera, *Coutarea*, *Coutaportla*, *Cubanola*, *Cigarrilla*, *Ceuthocarpus*, *Schmidtottia*, and *Siemensia*, display some combination of loculicidal and septicidal dehiscence together with septal splitting. Dehiscence may be limited mostly to the disc area as in *Cubanola* or may involve extreme septicidal dehiscence as in *Coutarea*; in all cases the actual spreading open of the capsule is made possible by septal splitting.

It should be noted that "dehiscence," as used above, refers to the condition of the capsule at the stage of seed release. After seed release, the

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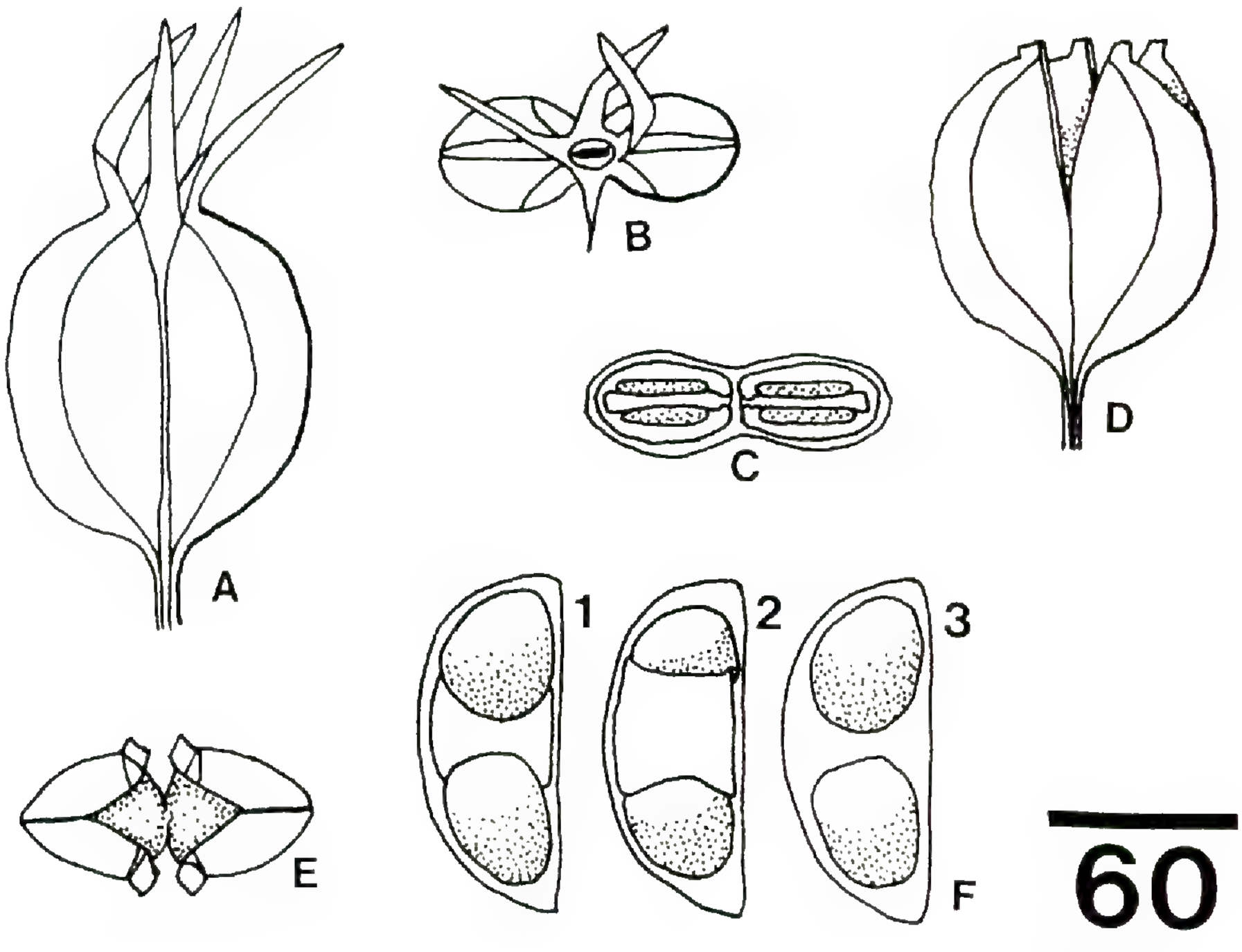
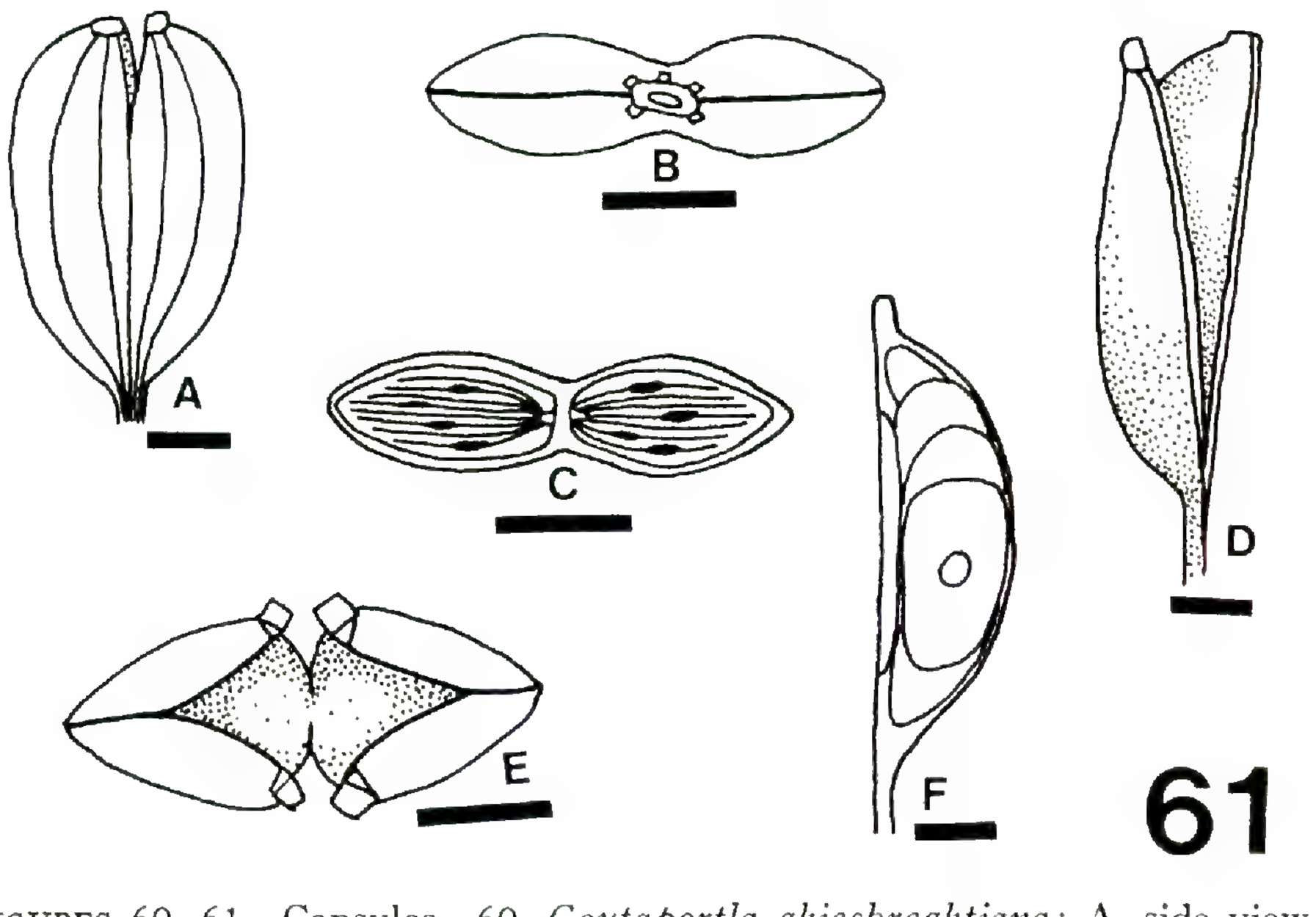
through middle, to show septum, large, spongy placenta, and imbricated, winged seeds; D, side view, showing early septicidal dehiscence; E, top view, to show early septicidal dehiscence; F, side view, locule after dehiscence, indicating complete septal separation and septal splitting, seeds showing through split septum. G, basipetally imbricated seeds in place on placenta (center). Bar scales = 5 mm.





FIGURES 60, 61. Capsules. 60, *Coutaportla ghiesbreghtiana*: A, side view; B, top view; C, cross section just below middle, to show septum, flattened placenta filling center of each locule, and seeds; D, side view, indicating method of dehiscence (loculicidal and septicidal); E, top view, dehiscence (loculicidal and septicidal), seen from above; F, side view of locule with wall removed to show placenta and seed arrangement (1, two seeds, one ascending, one descending from placenta (center); *2*, after two seeds removed, placenta covering second two seeds; 3, after placenta removed, two seeds remaining). 61, *Coutarea hexandra*: A, side view, to show early dehiscence; B, top view; C, cross section

capsule begins to deteriorate. A badly deteriorated capsule may split along new sutures in addition to those previously opened. For example, very old capsules of *Portlandia* may open along the septum, and the septal walls may separate somewhat; old capsules of *Cubanola* may open beyond the disc area. Except for *Hintonia* and possibly *Osa*, all of the genera mentioned above would show similar dehiscence if only very old capsules were examined.

The most important clues to distinguishing these genera from *Portlandia* and from each other lie in the nature of the placenta, the attachment of the seeds, and the seed coat pattern. Seed coat pattern will be discussed separately.

In *Portlandia* (FIGURE 53) and *Isidorea* (FIGURES 55, 56) the placentae are linear and adnate for their whole length to the midline of the septum. The seeds are compressed-angulate, have a persistent funicle, and are horizontal in their attachment (i.e., they are perpendicular to the long axis of the capsule). There are from 150 to more than 300 seeds per capsule in *Portlandia*, and approximately 20 in *Isidorea*.

Cubanola and *Thogsennia* also have compressed-angulate seeds that are horizontally attached. In *Cubanola* the placentae are round in cross section (FIGURE 57), and in *Thogsennia* they are twice forked (FIGURE 59).

Coutarea (FIGURES 61, 62), with its capsules compressed perpendicular to the septum, has linear placentae. The seeds, elliptic and much flattened, are oriented vertically (i.e., parallel to the long axis of the capsule but perpendicular to the septum). There are about 50 per capsule.

Hintonia (FIGURE 58) has large, spongy placentae that are almost entirely covered by the broadly elliptic, much-flattened, and basipetally imbricate seeds.

Cigarrilla (FIGURE 64) also has large, spongy placentae, but the seeds are wingless, circular, flattened, and acropetally imbricate, and cover the placentae except along the side away from the septum.

Ceuthocarpus (FIGURE 63) also has seeds that are flattened and acropetally imbricate, but these cover the placentae.

Osa (FIGURE 66) is somewhat of a mystery since it has been little collected and only one capsule was available for study. Because the placentae were dried out, their nature remains unknown, but it appears that if fresh or boiled they would be quite large. The seeds are few (16 to 20 per capsule), large, and plump; although basipetally appressed, they do not overlap.

In *Siemensia* (FIGURE 65) the placentae are kidney shaped in cross section. The tiny (1 mm. or less) seeds, which are perpendicular to the placentae, cover it except for the side opposite the septum. After the seeds fall, a small hole is left in the placenta where each was attached.

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through middle, to show septum, small placentae, and winged seeds; D, one locule after dehiscence, to show complete septal separation and splitting, and some loculicidal dehiscence; E, dehiscence (deeply septicidal, shallowly loculicidal), seen from above; F, side view of one locule with one wall removed to show seed arrangement. Bar scales = 5 mm.

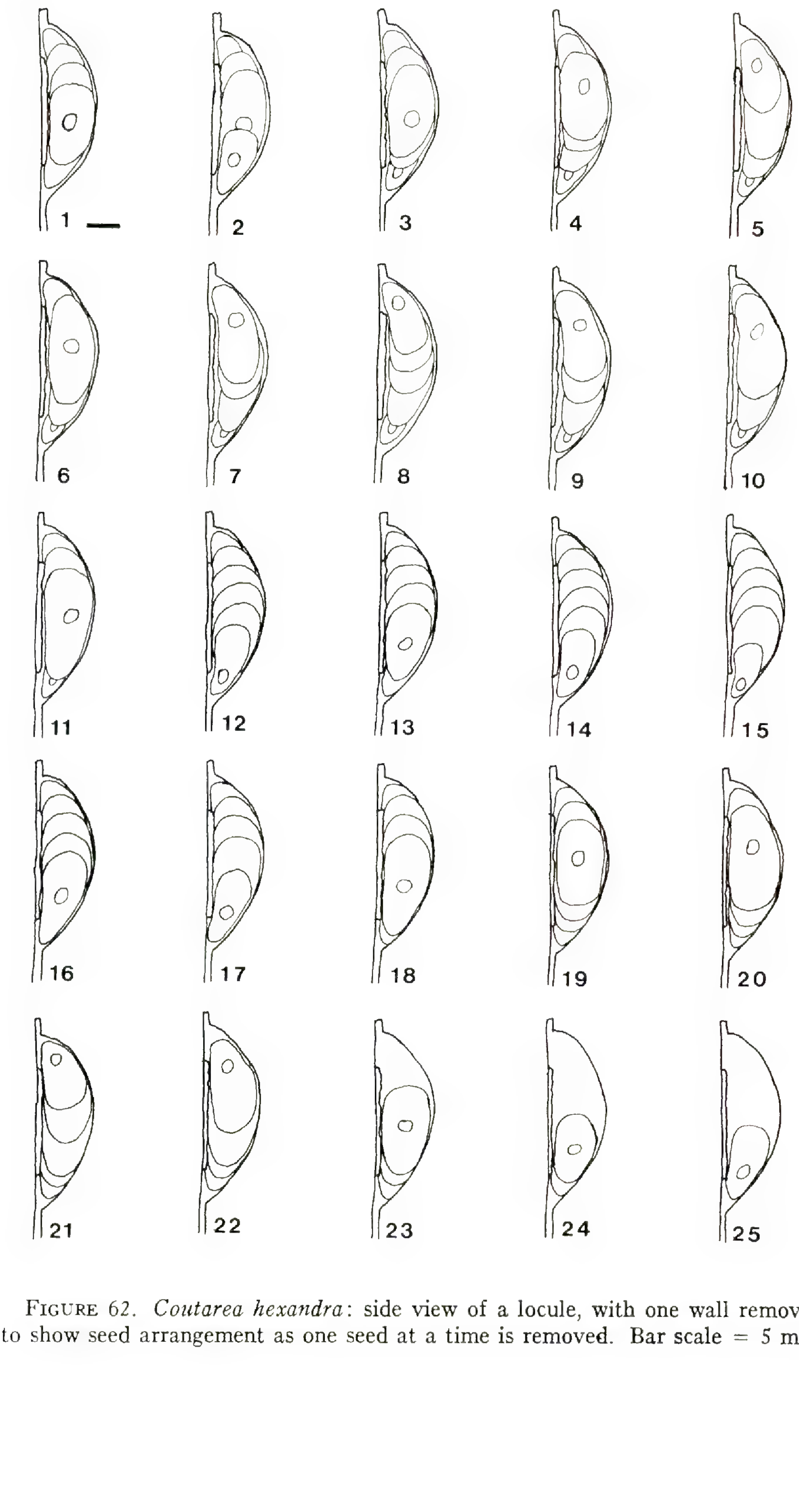
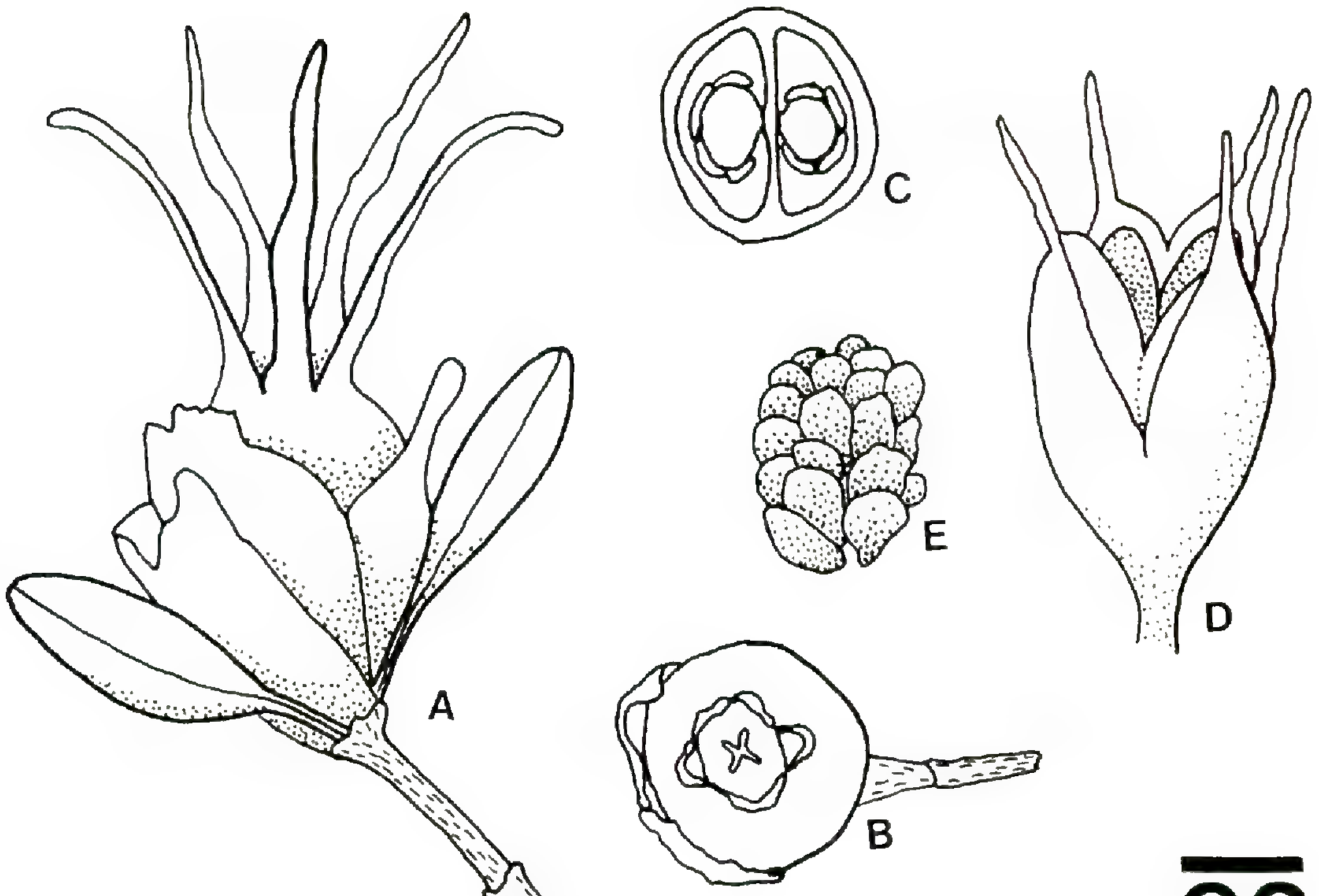


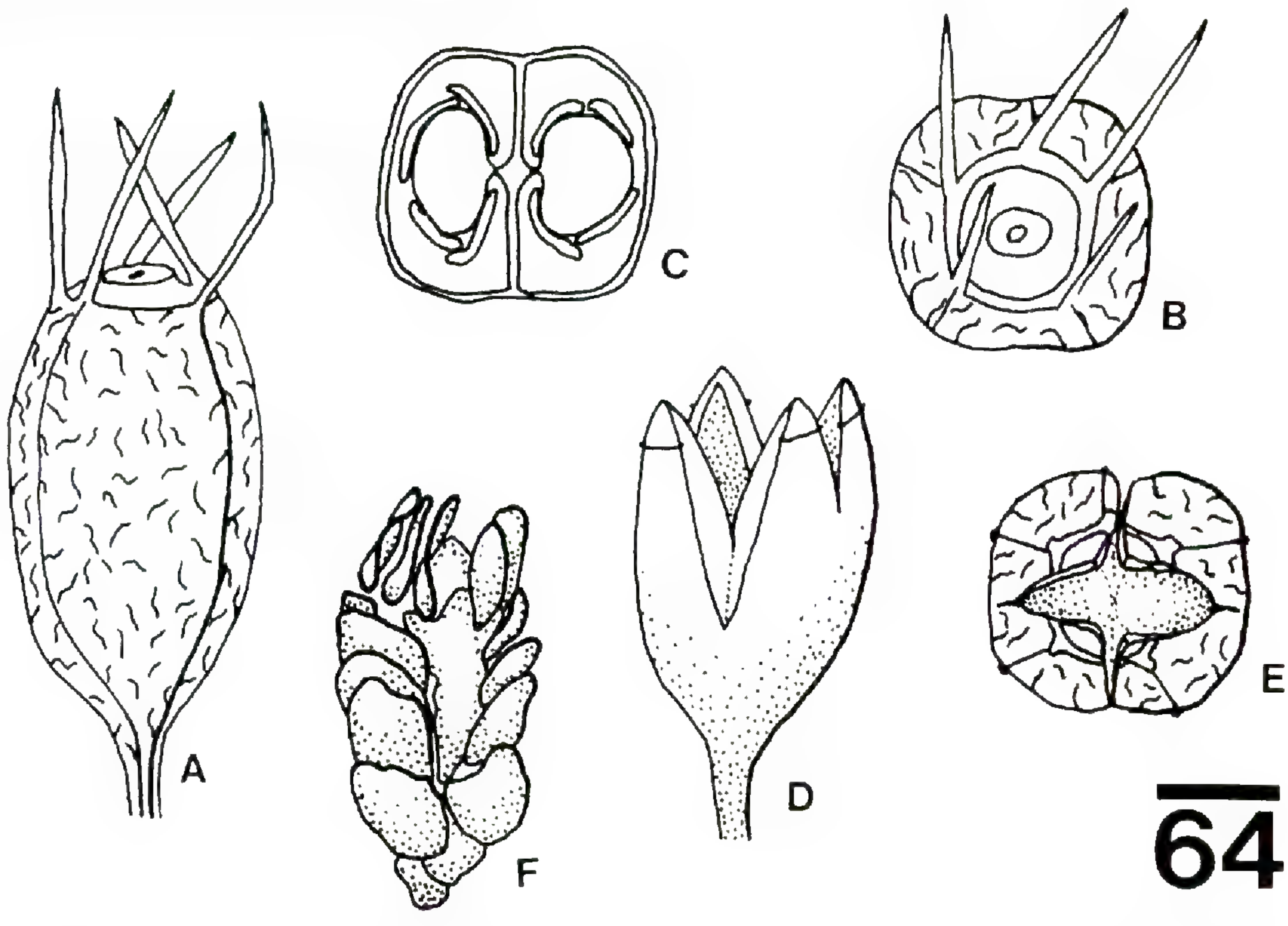
FIGURE 62. *Coutarea hexandra*: side view of a locule, with one wall removed to show seed arrangement as one seed at a time is removed. Bar scale = 5 mm.

TABLE 7. Distribution of important fruit and seed characters in Portlandia and associated genera.

GENUS	DEHISCENCE	FRUIT FLATTENED	FRUIT ENCLOSED IN INVOLUCRE	FRUIT PENDULOUS	SEEDS WINGED	FUNICLE PERSISTENT	PLACENTAE SMALL (CROSS SECTION)	PLACENTAE FORKED	SEEDS HORIZONTAL	PLACENTA CENTRAL WITH ASCENDING AND DESCENDING SEEDS	SEEDS IMBRICATED	SEEDS VERTICAL, PERPENDICULAR TO SEPTUM	SEEDS BASIPETALLY APPRESSED	APPROXIMATE NUMBER SEEDS PER LOCULE
Ceuthocarpus	l/s		+								A			20
Cigarrilla	l/s										A			30
Coutaportla	l/s	+								+				4
Coutarea	l/s	+		+		+						+		25
Cubanola	l/s								+					200
Hintonia	s			+							B			50
Isidorea	l				+	+			+					20
Osa	s?												+	10
Portlandia	l				+	+			+					150
Schmidtottia	l/s									+				14
Siemensia	l/s			+					+	+				60
Thogsennia								+	+					200

+ = Character present; blank space = character absent; ? = character questionably present; l = loculicidal; s = septicidal; A = acropetally; B = basipetally.





FIGURES 63, 64. 63, *Ceuthocarpus involucratus* (*Shafer 8282* (NY)). A–D, capsule: A, side view, to show calyx and subtending bracts; B, top view, older capsule, bracts and calyx worn away, early dehiscence (loculicidal and septicidal); C, cross section through middle, to show septum, placentae, imbricate seeds; D, side view, bracts removed, indicating method of dehiscence (loculicidal and septicidal). E, acropetally imbricated seeds in place on placenta (hidden). 64,

Schmidtottia and *Coutaportla* have several characters in common, although they are probably not related. Both have placentae attached to the center of the septum and extending across the locules, dividing them into upper and lower portions. The flattened seeds are arranged into two groups, one in the upper portion of each locule and ascending from the placenta, the other in the lower portion and descending from the placenta. In the case of *Coutaportla*, the capsule is much compressed perpendicular to the septum (FIGURE 60). There are usually only four seeds per locule, two in the upper portion and two in the lower. Occasionally there is a fifth seed in one of the portions. In *Schmidtottia* there are ten to fourteen seeds in each locule (five to seven in each portion) (FIGURE 54). Usually several seeds are attached down the sides of the placentae, giving a rather imbricate appearance. However, most are above or below the placentae, and all are perpendicular to the septum and parallel to the long axis of the capsule. The capsules are not flattened. In neither *Coutaportla* nor *Schmidtottia* are there any seeds attached to the sides of the placentae opposite the septum.

Placental shape and seed attachment and orientation are diagrammatically summarized in FIGURE 52.

The distribution of important fruit and seed characters for *Portlandia* and associated genera is shown in TABLE 7. On the basis of these characters, genera associated with *Portlandia* are quite distinct from both that genus and each other. *Portlandia*, *Isidorea*, *Cubanola*, and *Thogsennia*, with their horizontal seeds, and possibly *Osa* as well, belong to the Condamineeae. Based on the presence of raphides and multicellular uniseriate hairs, as well as on the numerous tiny seeds, *Siemensia* belongs to the Hedyotideae of the subfamily Rubioideae. *Coutarea* is best placed in the Cinchoneae because of its winged, vertical seeds. The positions of *Hintonia*, *Ceuthocarpus*, *Coutaportla*, *Cigarrilla*, and *Schmidtottia* are uncertain. None of the above placements can be made with great certainty since a large amount of work remains to be accomplished with regard to tribal relationships within the Rubiaceae.

SEEDS

Seed characters have been neglected in both floras and taxonomic revisions. This neglect is unfortunate since, in the few studies published, seed coat morphology has been shown to be helpful. A few of these studies have made use of seed pictures produced by the scanning electron microscope (SEM). Such pictures will likely become a routine tool in future taxonomic studies.

In the Rubiaceae, where tribal and generic characters are few and con-

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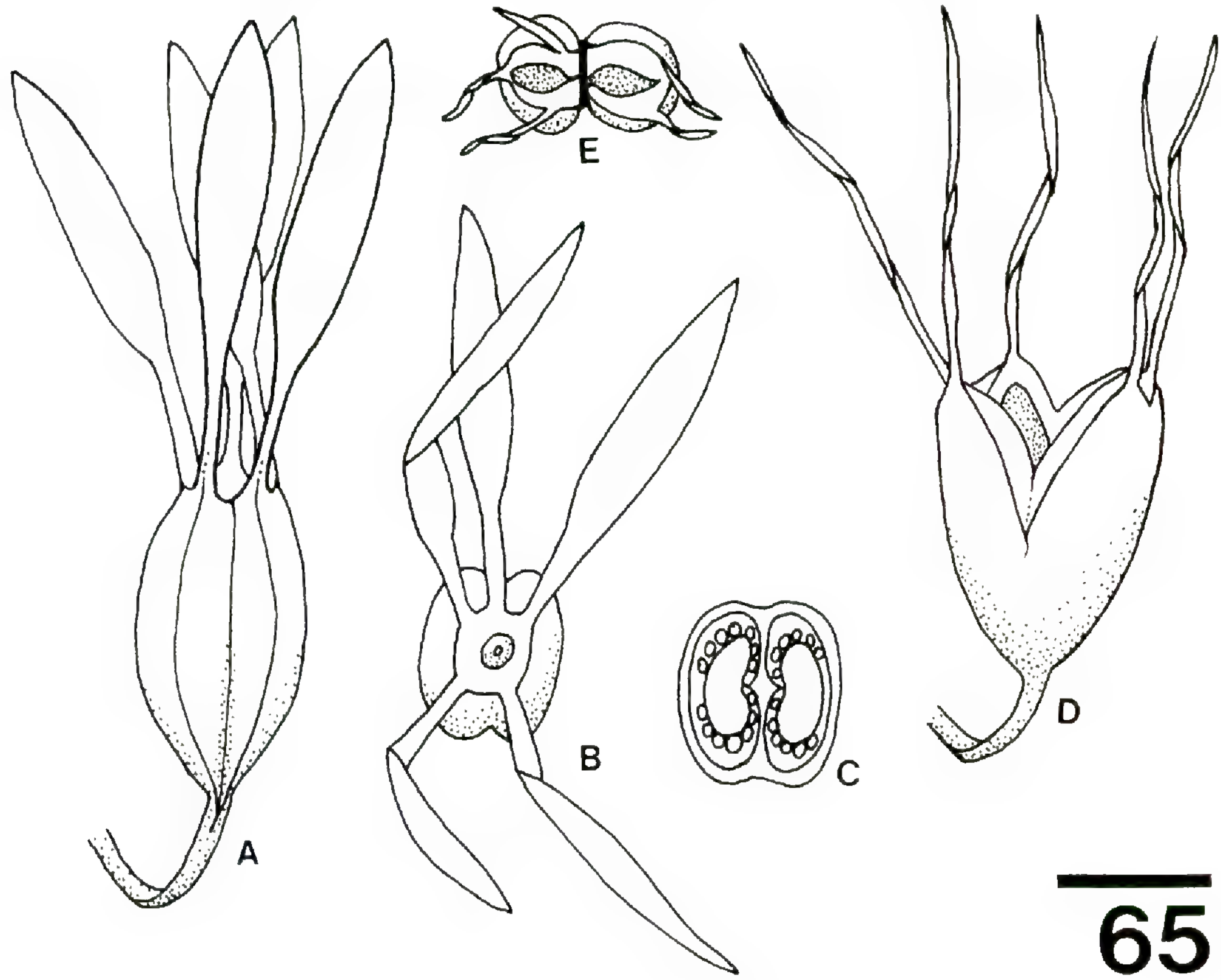
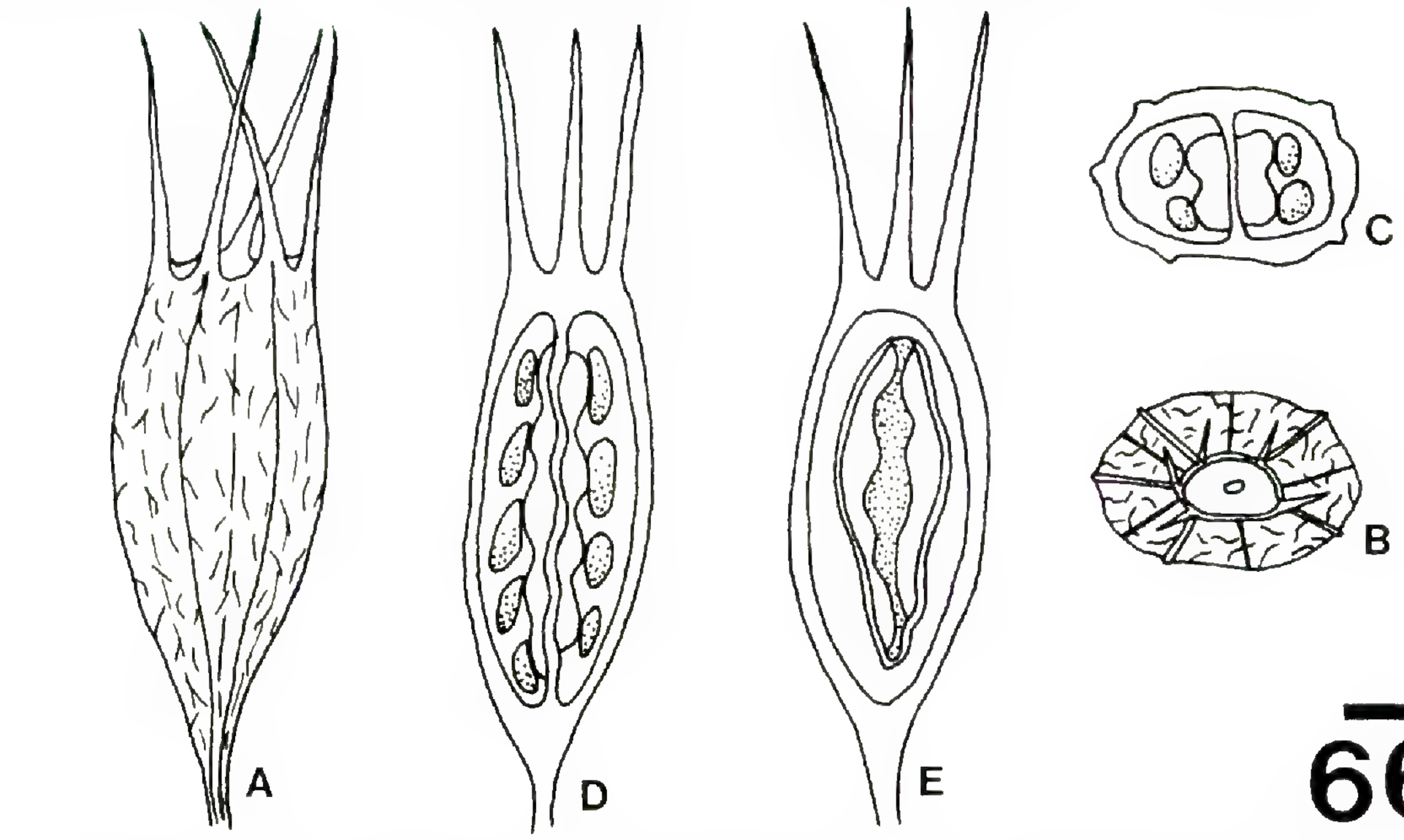
Cigarrilla mexicana. A–E, capsule: A, side view; B, top view; C, cross section through middle, to show septum, large placentae, imbricated seeds; D, side view, indicating method of dehiscence (loculicidal and septicidal); E, top view, to show early dehiscence (loculicidal and septicidal). F, acropetally imbricated seeds in place on spongy placenta (center), side view. Bar scales = 5 mm.





FIGURES 65, 66. Capsules. 65, *Siemensia pendula*: A, side view; B, top view; C, cross section through middle, septum, placentae, small seeds; D, side view, dehiscence (septicidal and loculicidal); E, top view, dehiscence (strongly septicidal, weakly loculicidal). 66, *Osa pulchra* (*Burger 7320* (F)): A, side view; B, top view; C, cross section, to show septum, placentae, seeds; D, side view, wall perpendicular to septum removed, showing septum, placentae, seeds; E, side view, wall parallel to septum removed, to show split septum with split placenta showing through slit. Bar scales = 5 mm.

troversial, seed coat characters may be of considerable value; in conjunction with other characters, they might eventually prove useful in detecting groups of related genera within many rubiaceous tribes.

Seeds of the major genera of the tribe Condamineeae (as well as those of several genera of the tribe Cinchoneae that have in the past been associated with *Portlandia*) were examined under the SEM for external morphological characters.

For examination under the SEM, seeds were removed from herbarium specimens and treated by the same methods as was the pollen (see that section). In addition, seeds of nine species were studied both by dissection and by serial sectioning. Sections made were 12 μm. thick.

For the most part, the seed testa terminology used has been modified after Murley (1951). In some cases where this terminology proved inadequate, modified pollen terminology was used.

The following descriptions are the result of the SEM studies.

Ceuthocarpus (FIGURE 79). Seeds somewhat flattened, broadly elliptic to obovate, 3–3.33 mm. long; testa reticulate.

Cigarrilla (FIGURE 80). Seeds somewhat flattened, elliptic to ovate, 3–3.4 mm. long; testa colliculate to low-tuberculate.

Coutaportla (FIGURES 81, 82). Seeds flattened, broadly elliptic, 3.2–3.5 mm. long; testa low-reticulate, with a baccate tubercle at one end of each cell.

Coutarea. Seeds flat, winged, elliptic, with slight indentation in wing at lateral attachment point, the central portion subcircular; testa reticulate, cells radiating from the center of the seed out to the periphery of the wing.

C. alba. Seeds 8.2 mm. wide (greatest dimension), central portion 3–3.2 mm. in diameter, wing 2.3–2.7 mm. wide laterally, 0.4 mm. wide on attachment side, and 0.8 mm. wide on side opposite attachment; testa cells mostly elongate.

C. hexandra (FIGURES 87, 88). Seeds 1.2 cm. wide, central portion 3.5–4 mm. in diameter, wing 3.5–4.5 mm. wide laterally, 1 mm. wide on attachment side, and 1.8–2 mm. wide on side opposite attachment; testa cells mostly isodiametric, with wavy walls.

Cubanola (FIGURE 74). Seeds elliptic to broadly elliptic, 3.1–3.5 mm. long; testa reticulate to foveolate.

Hintonia. Seeds flat, winged, obovate to broadly elliptic, with indentation at attachment point; central portion broadly elliptic to circular; testa reticulate, cells not radiating from central point.

H. latiflora (FIGURES 89, 90). Seeds 7 mm. long, central portion 2–3 mm. in diameter, wing 1.5 mm. wide.

H. octomera. Seeds 6.4 mm. long, central portion 2.2–2.9 mm. in diameter, wing 1.5–2.6 mm. wide.

H. standleyana. Seeds 6.2 mm. long, central portion 1.7–2.9 mm. in diameter, wing 0.9–1.7 mm. wide.

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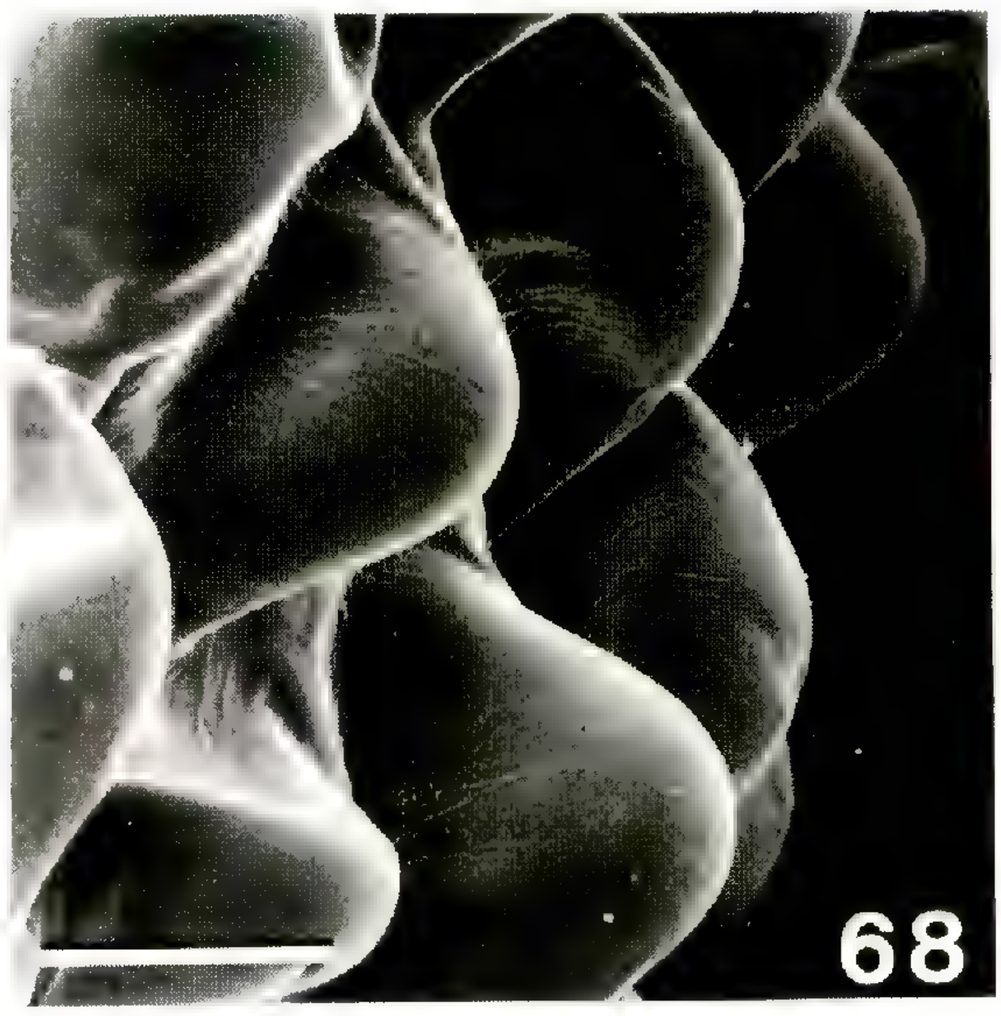

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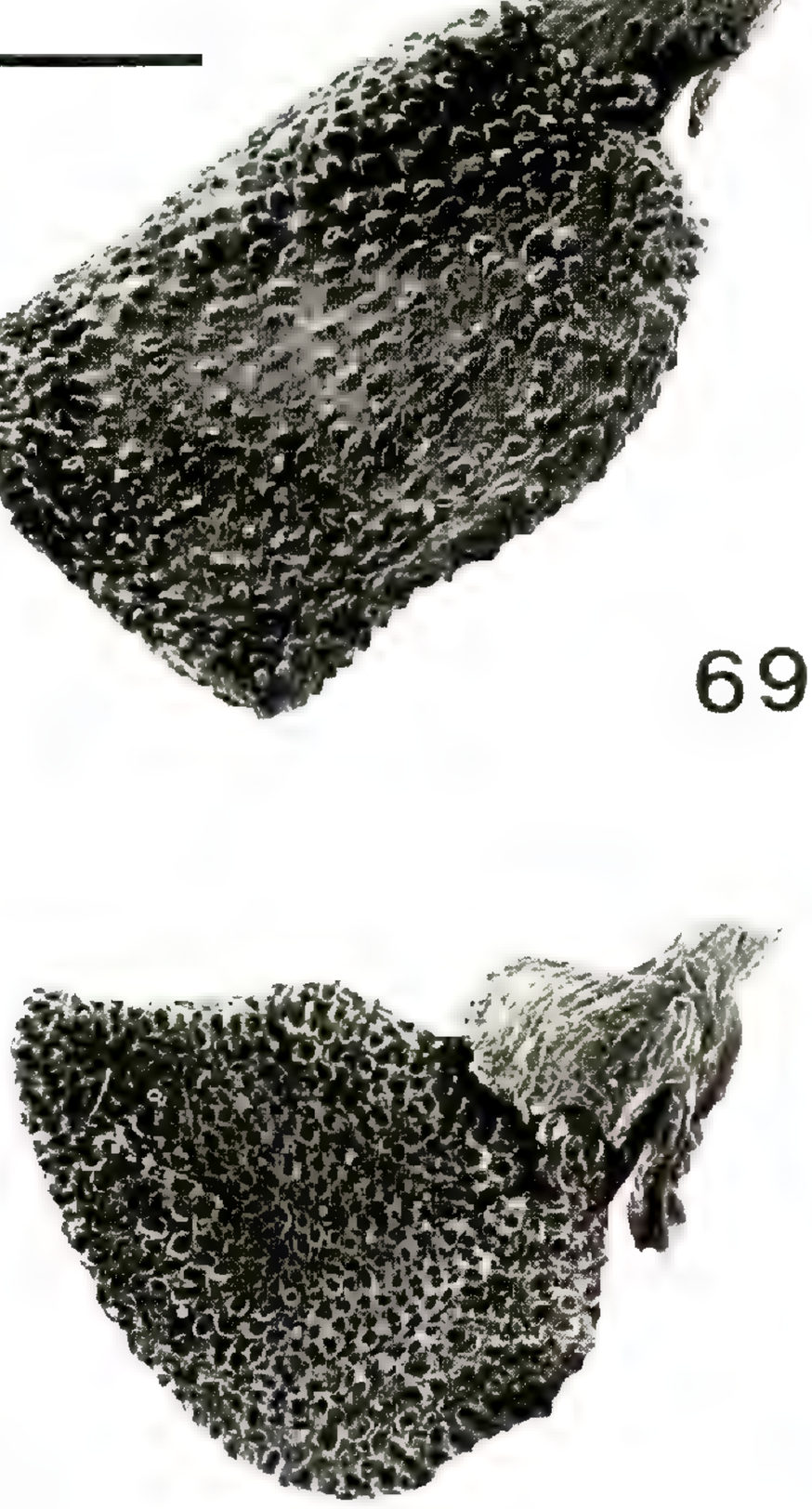

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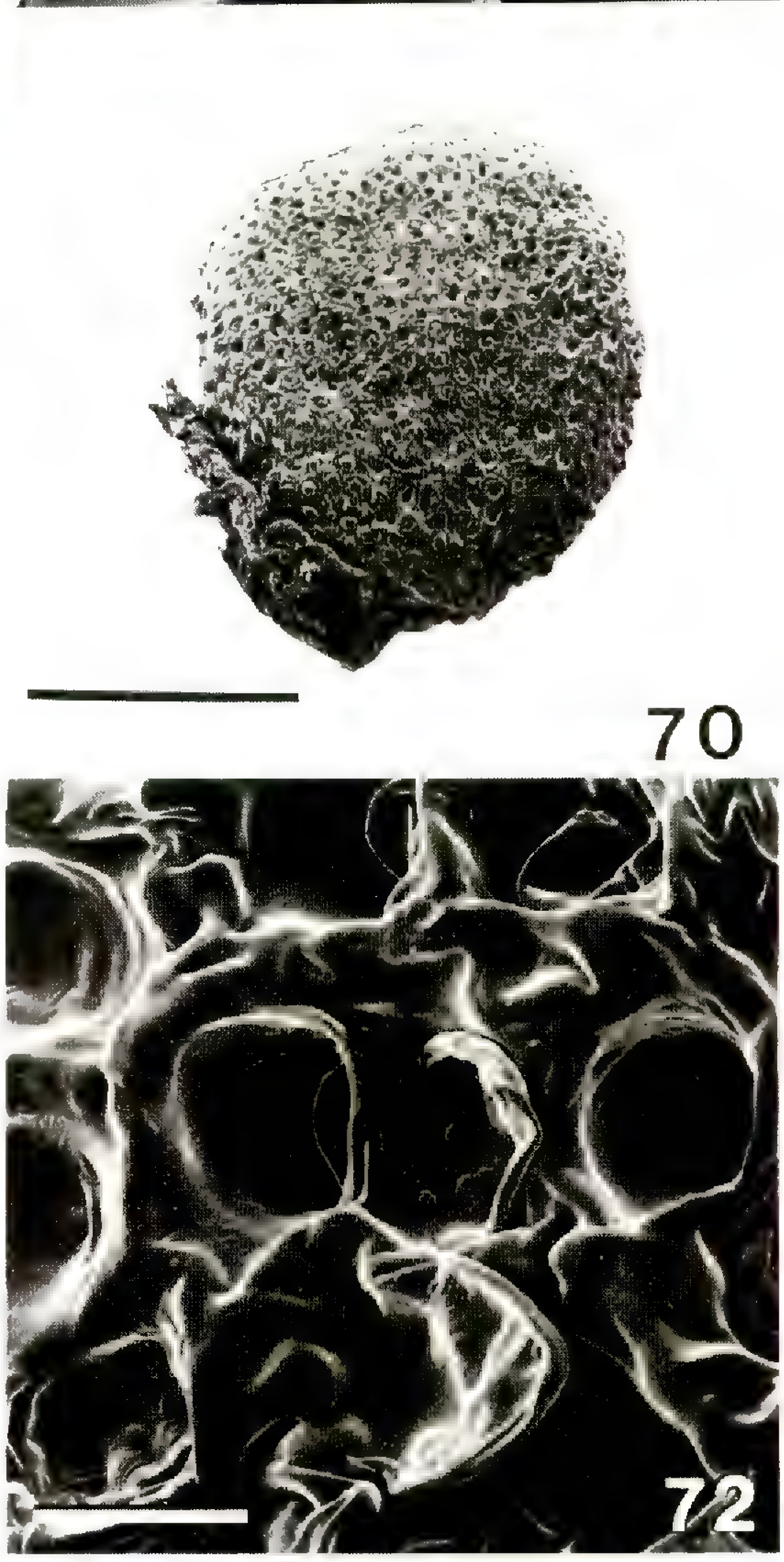

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FIGURES 67–72. Seeds: 67, 68, *Portlandia harrisii* (*Harris 11046* (US)); 69, *Portlandia grandiflora* (*Morton 715* (NY)); 70, *Isidorea leptantha* (*Ekman 15431* (A)); 71, 72, *Isidorea brachycarpa* (*Morton 9733* (US)). Bar scales = 1 μm. (67, 69–71) and 5 mm. (68, 72).

Isidorea (FIGURES 70–72). Seeds similar to those of *Portlandia*, but 1.5–3.2 mm. long.

Osa (FIGURE 73). Seeds plump, elliptic to broadly elliptic, 6.5 mm. long; testa mostly tuberculate but margins with colliculate areas; funicle (?) persistent.

Portlandia (FIGURES 67–69). Seeds compressed and angulate due to packing, elliptic to obovate, 2.5–3.5 mm. long; testa tuberculate with the tuberculae collapsed; funicle persistent and with cuplike swelling at apex.

Schmidtottia. Seeds somewhat flattened, elliptic to ovate or obovate, 2–2.9 mm. long; testa colliculate in *S. parvifolia* (FIGURE 78), *S. elliptica*, and *S. cubensis*, reticulate in *S. monantha*, *S. sessilifolia* subsp. *shaferi* (FIGURE 77), and *S. uliginosa*.

Siemensia (FIGURES 83, 84). Seeds broadly ovate to broadly elliptic, 0.9 mm. long; testa with closely packed, deep pits, interspaces densely granulate.

Thogsennia (FIGURES 75, 76). Seeds broadly obovate, 2.2–2.7 mm. long; testa collapsed-colliculate to reticulate, cells elongate and wrinkled.

Bikkia.

B. tetrandra. Seeds broadly elliptic to circular, 1.7 mm. long; testa reticulate, cells elongate and longitudinally oriented; large, clavate tubercles around the periphery coated with waxlike particles.

B. tubiflora. Seeds broadly elliptic to circular, 1.8 mm. long; testa reticulate, cells isodiametric, interspace margins granulate.

B. lenormandii. Seeds broadly elliptic, 2.3 mm. long; testa reticulate, cells isodiametric.

B. marianensis. Seeds obovate to obtriangular, 1.3 mm. long; testa reticulate, cells elongate and longitudinally oriented.

Calderonia. Seeds very thin, elliptic with one flat side, 1.6 cm. long; testa reticulate, cells isodiametric and collapsed with the thin outer walls in various stages of adhesion to the innermost ones.

Chimarrhis. Seed attachment peltate.

C. cymosa. Seeds broadly elliptic, 0.5–0.7 mm. long; testa deeply reticulate, the cells obliquely deepened, reticulate-thickened, radially arranged on attachment side of seed and randomly arranged on other side.

C. latifolia. Seeds elliptic, 0.5–0.7 mm. long; similar to *C. cymosa* except testa cells scalariform-thickened.

C. turbinata. Seeds elliptic to broadly elliptic, 0.9–1.6 mm. long; similar to *C. cymosa* and *C. latifolia* except for size and testa cells, which are not as deep and are reticulate-foveate-thickened.

Condaminea. Seeds narrowly obovate with truncate distal end, 0.6 mm. long; testa reticulate, cells elongate and longitudinally oriented, interspaces faintly granulate.

Exostema (FIGURES 85, 86). Seeds winged, flattened, elliptic, 3.9 mm. long, the seed portion large in proportion to wing, which varies in width from 3 mm. to 7 mm.; testa reticulate.

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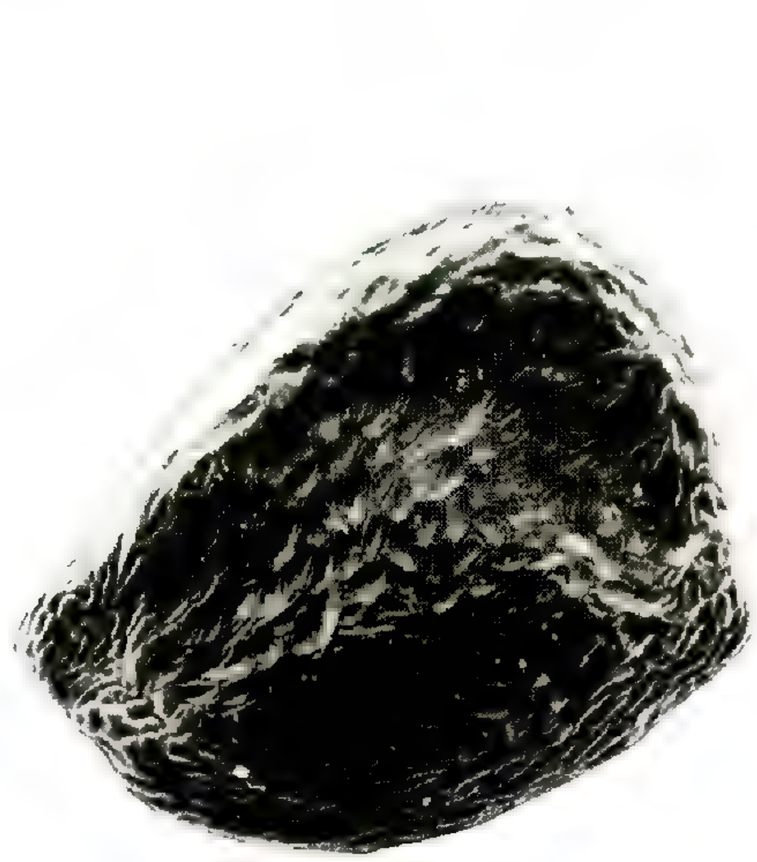

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FIGURES 73–78. Seeds: 73, *Osa pulchra* (*Burger 7320* (F)); 74, *Cubanola daphnoides* (*Clemente 4942* (NY)); 75, 76, *Thogsennia lindeniana* (*Shafer 1417* (NY)); 77, *Schmidtottia sessilifolia* var. *shaferi* (*Shafer 4180* (US)); 78, *Schmidtottia parvifolia* (*Alain 3592* (NY)). Bar scales = 1 mm. (73–75, 77, 78) and 50 μm. (76).

Picardaea. Seeds obovate with truncate distal end, 0.5–0.7 mm. long; testa strongly reticulate, interspaces strongly granulate.

Pinckneya. Seeds flat, depressed-obovate, with cleft at lateral attachment

point, 8 mm. long; testa reticulate, with tendency for cells to be arranged radially from point of attachment, interspaces faintly scalariform-reticulate-thickened.

Pogonopus. Seeds obovate with truncate distal end, 0.5 mm. long; testa strongly reticulate, cells somewhat elongate, interspaces faintly granulate.

Rustia. Seeds broadly obovate, 1.9 mm. long; testa shallowly reticulate.

Tresanthera. Seeds narrowly obovate to obtriangular, 0.9–1.4 mm. long; testa reticulate, cells elongate and longitudinally oriented, interspaces sparsely granulate around margins.

Within the tribe Condamineeae, seed orientation is horizontal in relation to the placenta. Except in *Chimarrhis*, which has peltate seeds, the attachment point on the seed is terminal. Seed shape and size and testa patterns are quite variable.

On the basis of the three genera studied (*Coutarea*, *Exostema*, and *Hintonia*), the Cinchoneae show much variation as to seed orientation and attachment. The seeds tend to be elongate and winged and to have a reticulate testa pattern.

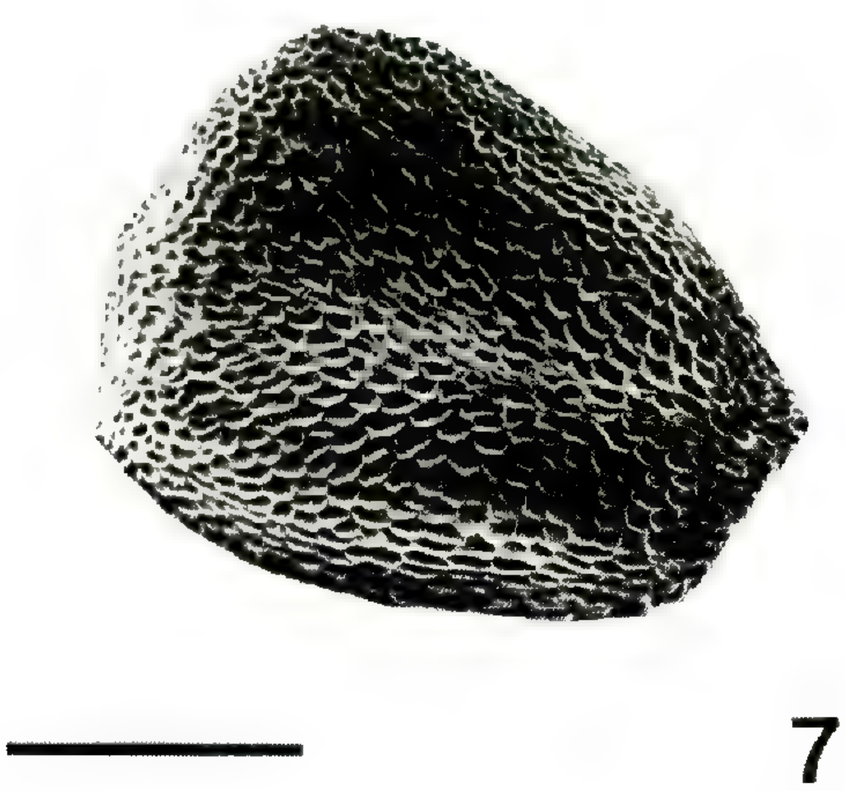
Within the Condamineeae, *Portlandia* and *Isidorea* are closely related genera. In both, the seeds are somewhat compressed and have a tuberculate surface. The tubercles tend to collapse during normal drying, resulting in some distortion of the original pattern. The funicle is persistent and bears a distinctive, basal, cuplike outgrowth that surrounds the base of the seed. The species belonging to these genera cannot be readily distinguished by their seeds.

On the basis of seed morphology, *Cigarrilla mexicana* (formerly *Portlandia mexicana*), with its flattened, colliculate seeds that lack a persistent funicle, does not belong in *Portlandia*; nor does *Osa pulchra* (formerly *Hintonia pulchra*) belong in the genus *Hintonia* as originally described. Except for their large size, the plump, wingless seeds of *Osa* are very similar to those of *Portlandia* and *Isidorea*. The seeds of *Hintonia*, on the other hand, are extremely flattened, wide-winged, and finely reticulate; unlike those of *Osa* and the rest of the Condamineeae, they are ascending and imbricate. It is not yet clear whether the origin of the seed appendage in *Osa* is funicular or placental.

Coutaportla ghiesbreghtiana and *Siemensia pendula* were originally described in *Portlandia*. Their seed testa patterns support Urban's view that each represents a monotypic genus. The seeds of *Coutaportla* are reticulate-foveolate and are unique in having a collapsed tubercle at one end of most cells. *Siemensia* seeds are minute, and their large, deep pits are densely granulate.

Five of the ten species of *Schmidtottia* were originally described in *Portlandia*. Here again, seed testa morphology supports Urban's decision to erect a new genus. All seven species studied have reticulate-areolate to somewhat colliculate seed testa patterns that are distinct from those of other genera in the Condamineeae, with the exception of *Ceuthocarpus*.

Thogsennia lindeniana has been placed at times in *Portlandia* and at other times in a genus with *Cubanola daphnoides*. Its seeds are most like



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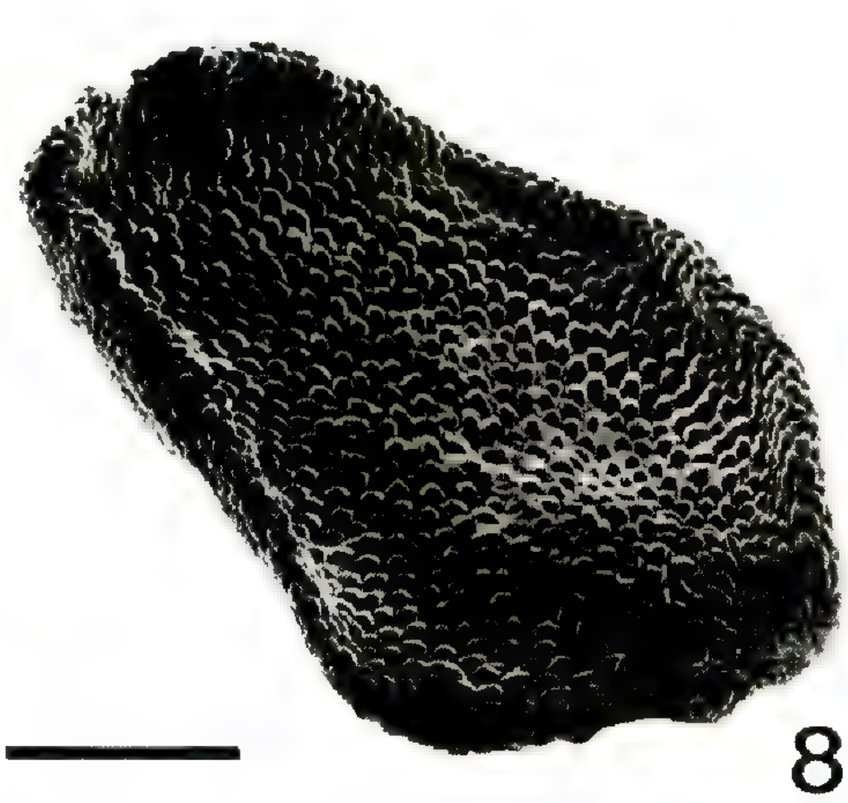

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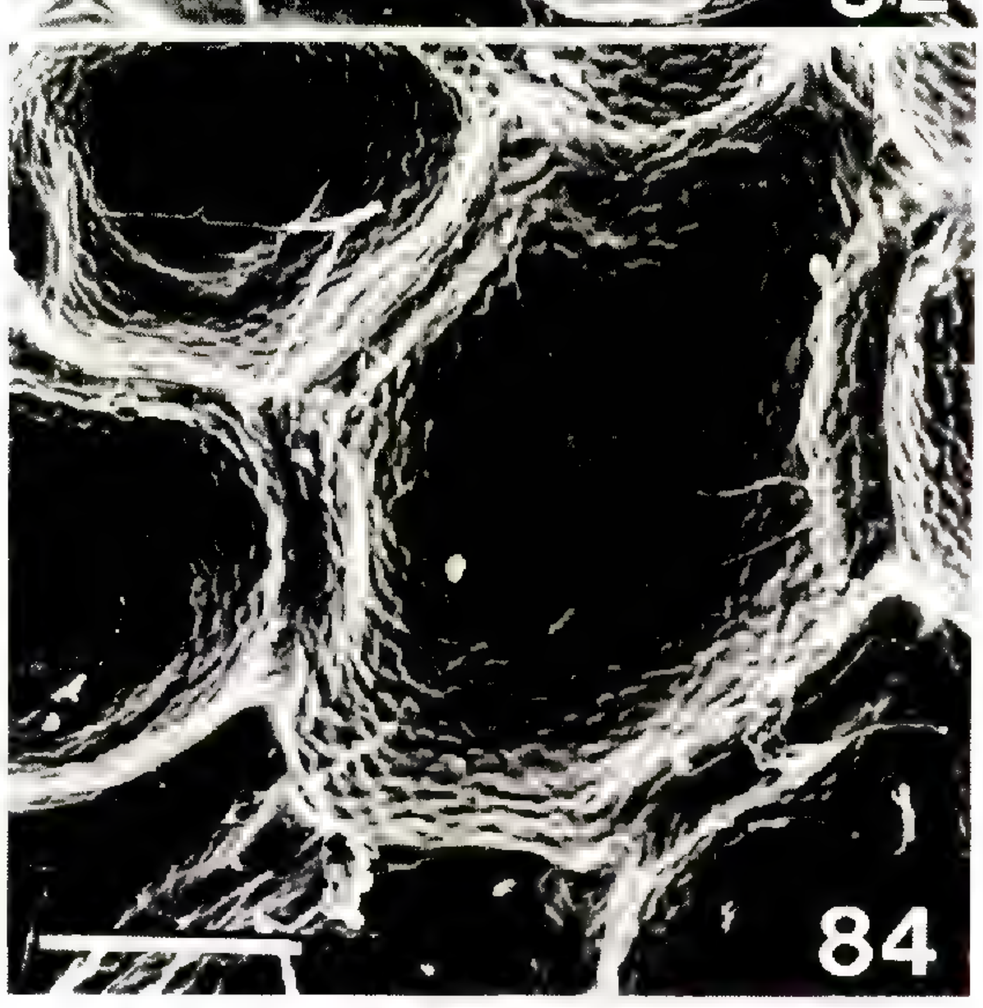

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FIGURES 79–84. Seeds: 79, *Ceuthocarpus involucratus* (*Clemente 3859* (GH)); 80, *Cigarrilla mexicana* (*Purpus 5042* (GH)); 81, 82, *Coutaportla ghiesbreghtiana* (*Conzatti 249* (GH)); 83, 84, *Siemensia pendula* (*C. Wright 2677* (GH)). Bar scales = 1 mm. (79–81), 50 μm. (82, 84), and 500 μm. (83).

those of *Schmidtottia* but differ in being heavier and thicker and in having testa cells that are elongate, irregular, and not as completely collapsed.

The seeds of *Tresanthera*, *Condaminea*, and *Pogonopus* are elongate-reticulate and granulate, while those of *Siemensia* and *Picardaea* are isodiametric-reticulate and strongly granulate. Seeds of *Rustia* are isodiametric-reticulate but not granulate.

Bikkia shows a great deal of seed testa variation. Seeds of *B. tetrandra* are distinctive with their large, clavate, peripheral tubercles, as are those of *B. tubiflora* with their nearly circular shape and their granular interspaces. The other two species are distinguished from one another by the shapes of their seeds and their testa cells.

Chimarrhis and *Pinckneya* both have thickenings within the interspaces of the testa cells. There the resemblance ends: *Chimarrhis* seeds are minute (0.5–1.6 mm.) and peltate, while those of *Pinckneya* are large (8 mm.) and have lateral attachment. *Chimarrhis* is unique in having obliquely deepened testa cells.

The seeds of *Calderonia* are in a class by themselves. Their extreme size (1.6 cm.) and wafer thinness make them distinctive even to the unaided eye.

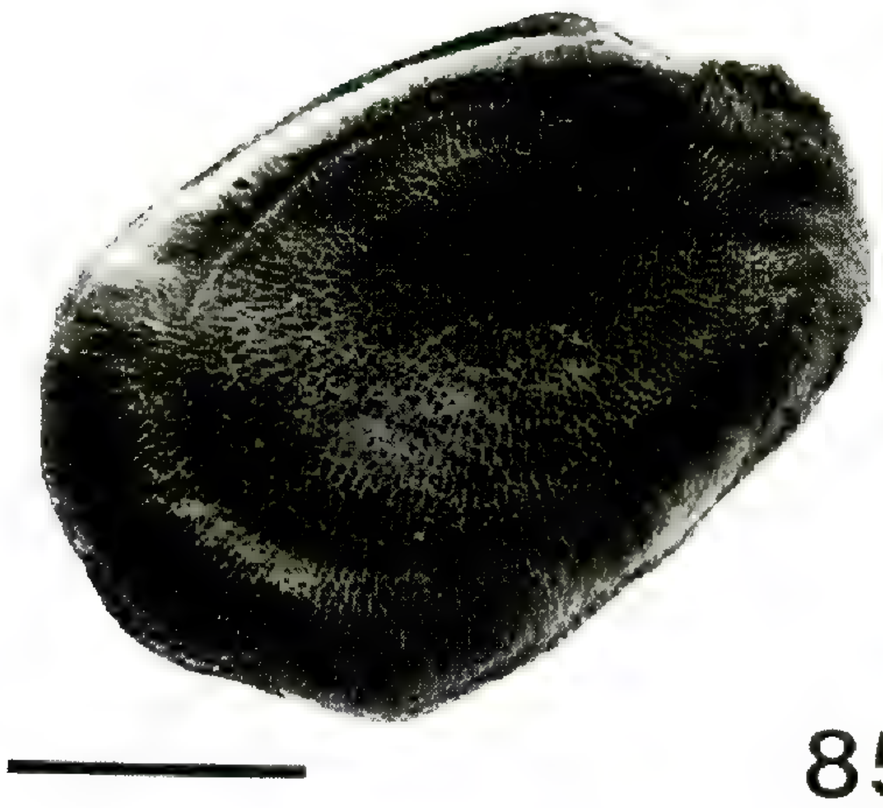
Seed sections indicated that in all nine cases studied, the testa pattern corresponds to the pattern of cells beneath; that is, one tubercle, or one apparent cell, coincides with one cell of the testa. In all cases the seeds were anatropous, and the embryos fell into the "axile," "foliate," and "spatulate" categories of Martin (1946), in that the embryo is centrally located in the endosperm of the seed, the cotyledons are expanded and wider than the stalk, and the embryo is erect. See Corner (1976) and Fagerlind (1937) for discussions of seed anatomy in the Rubiaceae.

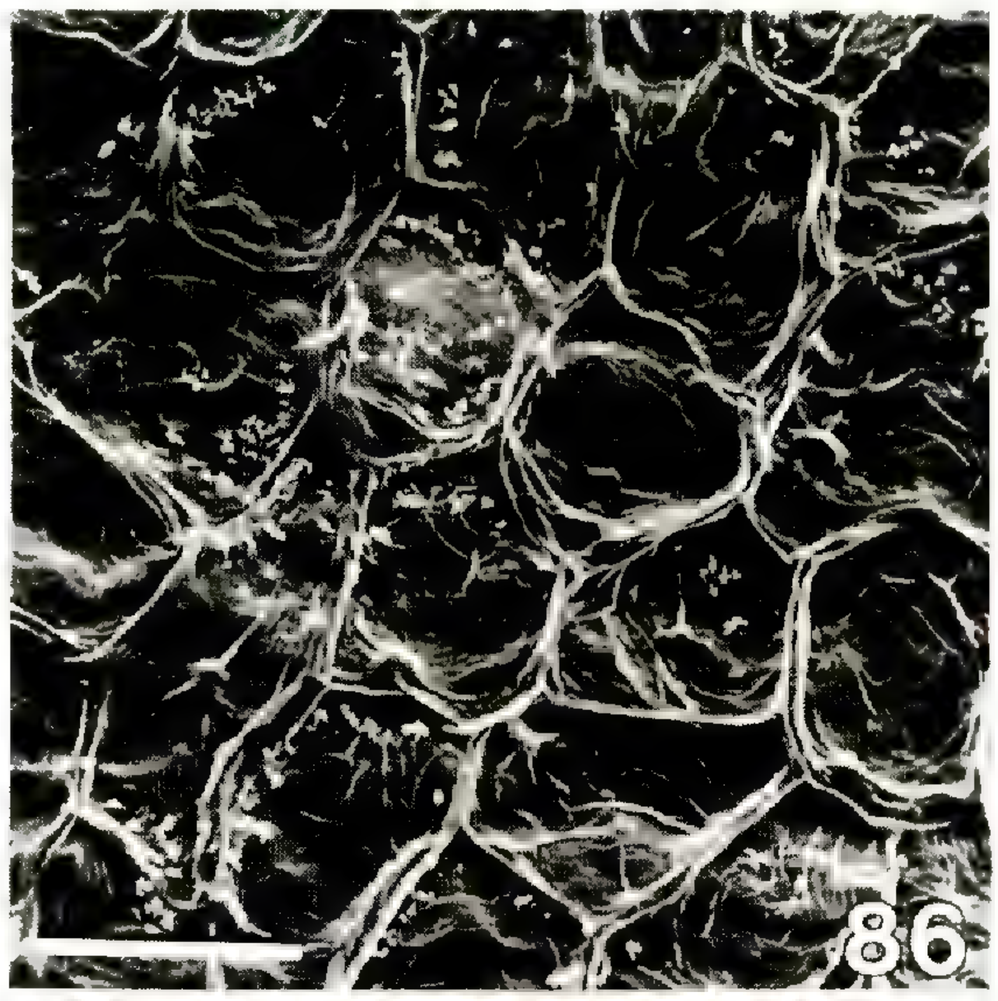
Except for *Osa*, which has large seeds and a sizable embryo with conspicuous venation, the genera and species investigated had embryos that were very similar in size and shape (TABLE 8).

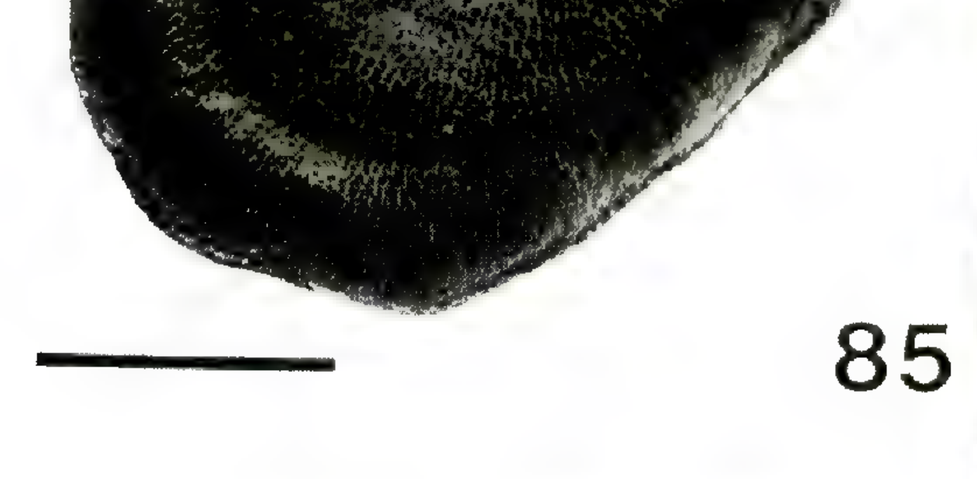
TABLE 8. Summary of three measurements of embryo size for nine taxa studied.

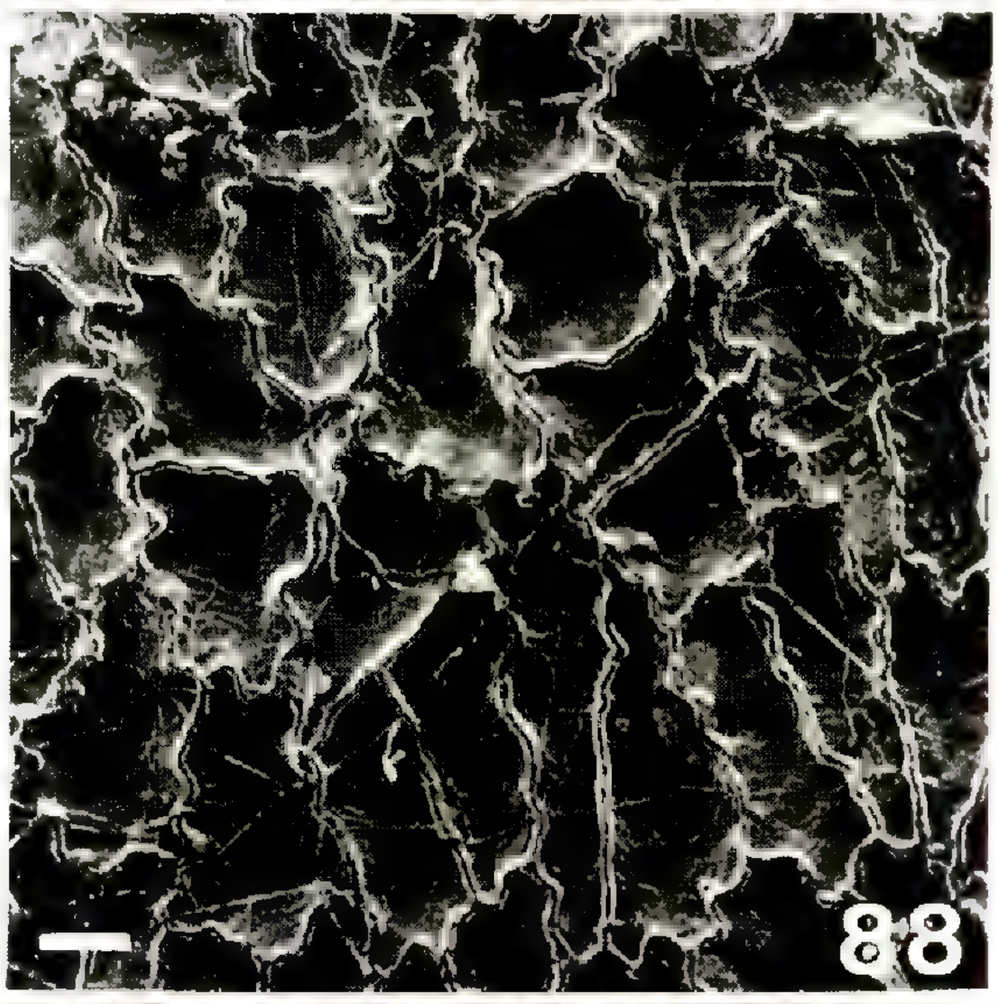
TAXON	MEASUREMENTS		
	Length of embryo	Width of cotyledons	Width of hypocotyl
Cigarrilla mexicana	2.04	0.52	0.28
Coutaportla ghiesbreghtiana	2.20	0.68	0.24
Cubanola daphnoides	2.20	0.60	0.24
Osa pulchra	4.80	2.00	0.44
Portlandia coccinea	1.68	0.48	0.20
Portlandia grandiflora	1.76	0.56	0.24
Portlandia harrisii	1.45	0.48	0.28
Schmidtottia elliptica	1.48	0.44	0.20
Thogsennia lindeniana	1.56	0.60	0.26

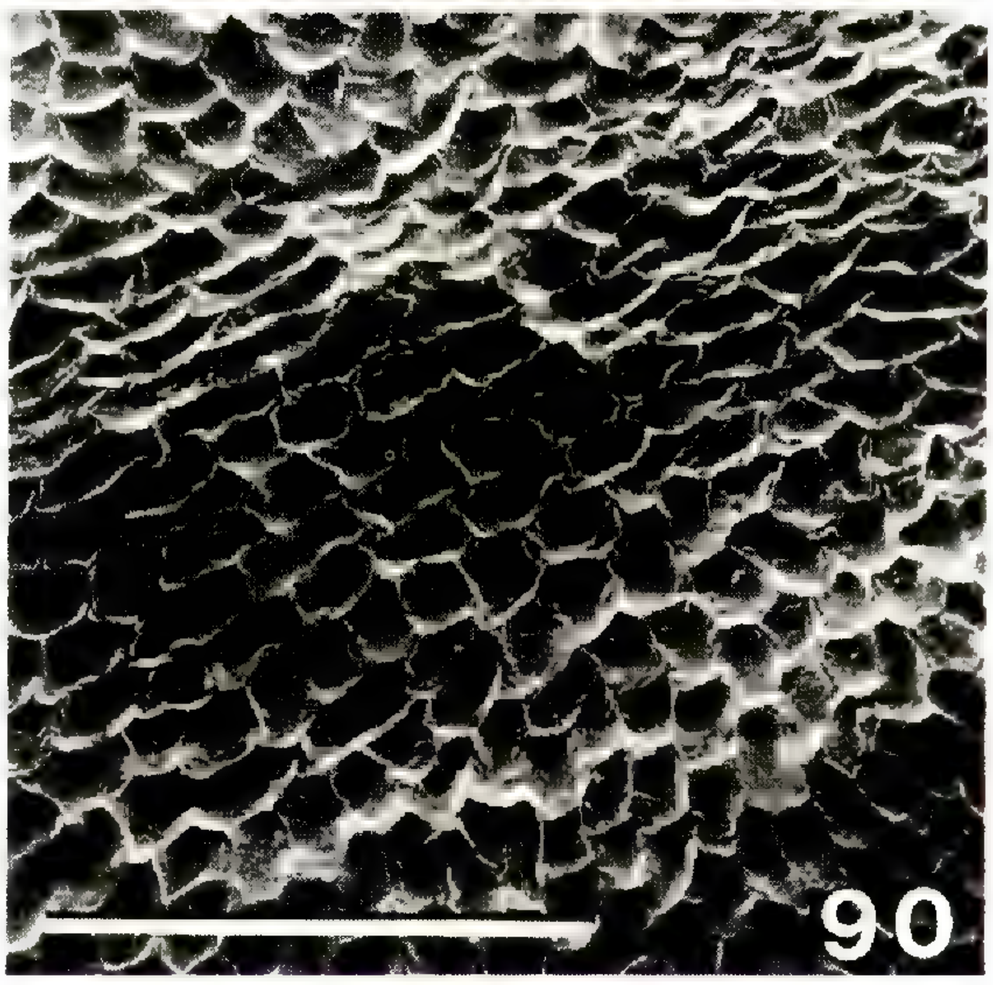
* All measurements are in mm.











FIGURES 85–90. Seeds: 85, 86, *Exostema caribaeum* (*Caldwell 8773* (A)); 87, 88, *Coutarea hexandra* (*Alston 10973* (F)); 89, 90, *Hintonia latiflora* (*Ortega 6832* (F)). Bar scales = 1 mm. (85, 87, 89), 50 μm. (86, 88), and 500 μm. (90).

Certainly seed testa pattern is of some value at the generic level, but whether there is correlation between seed types and tribal characters re-

mains to be seen. The tribes Condamineeae, Cinchoneae, and Rondeletieae are in need of revision as a group. The use of such new characters as pollen and wood anatomy should help to clarify their true relationships; seed orientation and attachment may also prove useful in this endeavor.

WOOD ANATOMY

The wood structure of the Rubiaceae is surprisingly uniform for such a large group (Chang, 1951). In addition, transitional cell types are common, often making it difficult to distinguish vessels from fibers. For these reasons, wood structure does not offer a useful set of taxonomic characters at the specific or the generic level. At the tribal level, however, wood structure has been shown to be of some value (Koek-Noorman, 1969a, 1969b, 1970, 1972).

Using cluster analysis, Koek-Noorman and Hogeweg (1974) made a numerical taxonomic study of wood variation in the Cinchoneae, Condamineeae, and Rondeletieae. This technique revealed two sets of highly correlated characters in the groups studied: 1) fiber tracheids, many vessels in (short) radial multiples, parenchyma lacking — or scanty and paratracheal, and crystal sand present in ray cells; and 2) libriform fibers, vessels solitary, parenchyma diffuse-reticulate, and crystal sand absent.

He found that each of the three tribes studied could be divided into two groups corresponding to these two sets of wood characters. A combined analysis of all three tribes together gave the same results: two distinct groups displaying the same two sets of characters as before. These results suggest that the key to understanding any one of the three tribes may be the simultaneous study of all three, using a number of approaches (e.g., wood anatomy, and pollen, seed, and fruit structure). Two tribes might conceivably emerge in place of the present three.

During the present study, the wood of four species of *Portlandia* was examined to determine the range of variation present within the genus and to enable comparison with the wood structure of the Rubiaceae as a whole. The wood of *Cigarrilla* was also examined. Wood samples of the other taxa under study were not available for sectioning.

Each of the specimens collected included wood with bark, and voucher specimens with leaves, flowers, and fruits. It should be noted that the wood of both *Portlandia harrisii* and *Cigarrilla* was still young and contained pith. The wood samples and microscope slides made from them are in the Harvard Wood Collection at the Botanical Museum (Hw), and voucher specimens are in the herbarium of the Arnold Arboretum, both at Harvard University.

Wood samples were cut into blocks approximately 1 cm.^{2} and were boiled in water for one hour. The blocks were then placed in hydrofluoric acid for one to two weeks and, when soft, cut into sections 15–20 μm. thick on a sliding microtome. The sections were stained in saffranin and mounted in diaphane on glass slides. Macerations were made by boiling wood slivers in water and then placing them in a mixture of equal portions of 10 percent

nitric acid and 10 percent chromic acid (Jeffrey's solution) overnight. The macerations were stained in saffranin and mounted in diaphane.

In examining and describing wood structure, the following sample sizes were used:

MEASUREMENT	SAMPLE SIZE FOR EACH SPECIES	SAMPLE SIZE FOR THE GENUS PORTLANDIA
Vessel tangential diameter	25	100
Vessel density	10	40
Vessel element length	25	100
Ray height	25	100
Ray density	10	40

Important wood measurements for the samples studied are given in TABLE 9.

TABLE 9. **Summary of wood measurements.**

TAXON	MEASUREMENT				
	Vessel density per mm.^{2}	Average vessel diameter (μm.)	Average vessel element length (μm.)	Average ray density per mm.	Average ray height (μm.)
Portlandia	288	20	677	15	472
P. coccinea					
var. *coccinea*	261	24	809	15	508
var. *proctorii*	285	17	761	14	457
P. grandiflora	152	21	689	12	485
P. harrisii	455	22	448	18	438
Cigarrilla mexicana	566	18	470	14	418

Portlandia P. Browne

Growth rings. Indistinct. Wood diffuse-porous, fairly hard.

Vessel elements. Mostly solitary, but some multiples and/or tangential banding may be present at beginning of growth rings; average density 288 vessels per mm.^{2} (range 111 to 642 vessels per mm.^{2}, standard deviation (s) 132 vessels per mm.^{2}); average vessel diameter 20 μm. (range 9–33 μm., s 6 μm.); average vessel element length 677 μm. (range 221–1104 μm., s 207 μm.); perforation plates always simple; end wall slope 45°, extensions rarely elongate; intervascular pitting alternate, minute.

Parenchyma. Apotracheal-diffuse, scanty; crystals rare, only rhombic ones seen.

Imperforate tracheary elements. Libriform fibers with slightly bordered pits and oblique apertures predominate.

Rays. Heterocellular; uniseriate to triseriate (in *P. coccinea* biseriate rays are short and have long uniseriate wings); average density 15 rays per mm. (s 3 rays per mm.); average ray height 472 μm. (range 83–1518 μm., s 289 μm.); vessel–ray pitting alternate, similar to intervascular.

Pith. Heterogeneous, with few large isodiametric cells, no plates or thickenings.

Portlandia coccinea Sw. (description based on *Aiello 1308* (A), Hw 30683).

Growth rings. Indistinct. Wood diffuse-porous.

Vessel elements. Mostly solitary but some multiples occasionally present; tendency for banding; average density 261 vessels per mm.^{2} (range 199 to 332 vessels per mm.^{2}, s 46 vessels per mm.^{2}); average vessel diameter 24 μm. (range 14–33 μm., s 5.4 μm.); average vessel element length 809 μm. (range 497–1104 μm., s 151 μm.); perforation plates simple; intervascular pitting alternate, minute.

Parenchyma. Apotracheal-diffuse, scanty.

Imperforate tracheary elements. Libriform fibers with slightly bordered pits and oblique apertures.

Rays. Heterocellular with both square and upright cells, or of upright cells only; uniseriate or short biseriate with long uniseriate wings; average density 15 rays per mm. (s 1.5 rays per mm.); average ray height 508 μm. (range 60 μm.–1242 μm., s 337 μm.); vessel–ray pitting alternate, similar to intervascular; globular inclusions present.

Portlandia coccinea var. **proctorii** Aiello (description based on *Aiello 1297* (A), Hw 30686).

Growth rings. Indistinct. Wood diffuse-porous.

Vessel elements. Solitary; average density 285 vessels per mm.^{2} (range 243 to 354 vessels per mm.^{2}, s 54 vessels per mm.^{2}); average vessel diameter 17 μm. (range 9–28 μm., s 5 μm.); average vessel element length 761 μm. (range 483–938 μm., s 145 μm.); perforation plates simple; intervascular pitting alternate, minute.

Parenchyma. Apotracheal-diffuse, scanty.

Imperforate tracheary elements. Libriform fibers with slightly bordered pits and oblique apertures.

Rays. Heterogeneous with both upright and square cells, or of upright cells only; uniseriate, biseriate, and triseriate in about equal numbers; average density 14 rays per mm. (s 2.5 rays per mm.); average ray height 457 μm. (range 166–1173 μm., s 261 μm.); vessel–ray pitting alternate, similar to intervascular.

Portlandia grandiflora L. (description based on *Aiello 1304* (A), Hw 30685).

Growth rings. Indistinct. Wood diffuse-porous.

Vessel elements. Mostly solitary; average density 152 vessels per mm.^{2} (range 11 to 221 vessels per mm.^{2}, s 35 vessels per mm.^{2}); average vessel

diameter 21 μm. (range 9–33 μm., s 5 μm.); average vessel element length 689 μm. (range 345–1035 μm., s 207 μm.); perforation plates simple; intervascular pitting alternate, minute.

Parenchyma. Apotracheal-diffuse, somewhat scanty to slightly banded.

Imperforate tracheary elements. Libriform fibers with slightly bordered pits and oblique apertures.

Rays. Heterogeneous with both square and upright cells, very few procumbent; mostly biseriate or uniseriate, rarely with some triseriate; average density 12 rays per mm. (s 2.3 rays per mm.); average ray height 485 μm. (range 41–1187 μm., s 240 μm.); vessel–ray pitting alternate, similar to intervascular.

Portlandia harrisii Britton (description based on *Aiello 1306* (A), Hw 30684).

Growth rings. Indistinct. Wood diffuse-porous.

Vessel elements. Solitary; wavy tangential banding; average density 455 vessels per mm.^{2} (range 310 to 642 vessels per mm.^{2}, s 128 vessels per mm.^{2}); average vessel diameter 22 μm. (range 9–28 μm., s 12 μm.); average vessel element length 448 μm. (range 221–635 μm., s 102.5 μm.); perforation plates simple; intervascular pitting alternate, minute.

Parenchyma. Apotracheal-diffuse, very sparse.

Imperforate tracheary elements. Libriform fibers with slightly bordered pits and oblique apertures.

Rays. Heterogeneous; mostly uniseriate, a few biseriate; average density 18 rays per mm. (s 3 rays per mm.); average ray height 438 μm. (range 96–1449 μm., s 319 μm.); vessel–ray pitting alternate, similar to intervascular.

Cigarrilla mexicana (Zucc. & Martius) Aiello (description based on *Aiello 1240* (A), Hw 30687).

Growth rings. Indistinct. Wood diffuse-porous.

Vessel elements. Solitary; occasional faint, narrow tangential banding; average density 566 vessels per mm.^{2} (range 442 to 664 vessels per mm.^{2}, s 66 vessels per mm.^{2}); average vessel diameter 18 μm. (range 9–23.5 μm., s 3 μm.); average vessel element length 470 μm. (range 276–787 μm., s 103 μm.); perforation plates simple; intervascular pitting alternate, minute.

Parenchyma. Apotracheal-diffuse, scanty.

Imperforate tracheary elements. Libriform fibers with slightly bordered pits and oblique apertures.

Rays. Heterocellular; mostly uniseriate, very few biseriate; average density 14 rays per mm. (s 3 rays per mm.); average ray height 418 μm. (range 55–1311 μm., s 277 μm.); vessel–ray pitting alternate, similar to intervascular.

Pith. Homogeneous, of isodiametric cells.

Within *Portlandia* there is very little variation in vessel diameter and

ray density. However, there is a great deal of variation in vessel density, vessel element length, and ray height within each specimen, as well as among the species. In *P. coccinea* var. *proctorii* the rays are distinctly 1- to 3-seriate, while in the other taxa they are uniseriate or biseriate with only a few triseriate. Except for details of ray composition, the wood structure of *P. coccinea* var. *coccinea* and *P. coccinea* var. *proctorii* are very similar.

Cigarrilla stands apart from *Portlandia* in having greater vessel density, rays almost entirely uniseriate with rare short biseriate ones, and pith homogeneous and made up of isodiametric cells instead of heterogeneous.

CYTOLOGY

Chromosome counts have been published for approximately 55 genera in 16 tribes of the Rubiaceae. TABLE 10 shows the distribution of the

TABLE 10. **Base chromosome numbers reported for four main subfamilies of the Rubiaceae.**

CINCHONOIDEAE	RUBIOIDEAE	IXOROIDEAE	GUETTARDOIDEAE
9	9		
10	10		
11	11	11	11
	12	12	
	14		
17		17	

base numbers reported for the four main subfamilies (Darlington, 1955). The number $n = 11$ occurs in all four subfamilies and is also the most common base number throughout the family.

The only published count for a species belonging to the tribe Condamineeae was made by Fagerlind (1937) on *Portlandia grandiflora* in cultivation at Kew Gardens. His count was reported as "$2n = 22$?"; no explanation for his uncertainty was given.

Because *Portlandia* flowers are both large and scarce, it is difficult to obtain flower buds at the proper stage for making chromosome counts, and, while buds were collected from four species, only one sample was collected during meiosis. That sample, from *P. platantha*, was taken from a plant growing near the Golden Head Beach Hotel, St. Mary Parish, Jamaica, on June 7, 1975. Flower buds were collected and preserved in Carnoy's Fixative (1 part glacial acetic acid : 3 parts chloroform : 6 parts absolute ethanol), and herbarium specimens (*Aiello 1302*) were made. Anthers were squashed in acetocarmine, and more than 15 separate counts were made on an anther 8 mm. long with chromosomes at metaphase II. The result was the same for all counts: eleven darkly staining chromosomes plus one lighter-staining one for a total of $n = 12$, a number not previously reported for the Cinchonoideae.

TABLE 11. **Results of test for presence of alkaloids in leaves.**

GENUS	SPECIES	SPECIMEN	RESULT
Ceuthocarpus	*involucratus* (Wernham) Aiello	*Alain 845* (GH)	–
Cigarrilla	*mexicana* (Zucc. & Martius ex DC.) Aiello	*Aiello 1225* (A)	+
Coutaportla	*ghiesbreghtiana* (Baillon) Urban	*Aiello 1262* (A)	f+
Coutarea	*hexandra* (Jacq.) Schum.	*Hassler 12191* (F)	–
Cubanola	*daphnoides* (R. Graham) Aiello	*Rugel 374* (NY)	f+
	domingensis (Britton) Aiello	*Rose 4176* (NY)	f+
Hintonia	*latiflora* (Sessé & Moç. ex DC.) Bullock	*Waterfall 12779* (MICH)	–
		Gentry 5700 (MICH)	–
	lumaeana (Baillon) Bullock	*Steyermark 47612a* (F)	–
	octomera (Hemsley) Bullock	*Lundell 7469* (MICH)	–
	standleyana Bullock	*Hinton 12004* (MICH)	–
Isidorea	*brachycarpa* (Urban) Aiello	*Ekman 15258* (US)	–
	leonardii Urban	*Eyerdam 56* (GH)	–
	oblanceolata (Urban) Aiello	*Ekman 9588* (S)	–
	polyneura (Urban) Aiello	*Ekman 15608* (BM)	–
Osa	*pulchra* (D. Simpson) Aiello	*Burger & Liesner 7320* (F)	–

Portlandia	*coccinea* Sw.	*Aiello 1300* (A)	+
		Aiello 1308 (A)	+
	grandiflora L.	*Aiello 1307* (A)	+
	harrisii Britton	*Aiello 1306* (A)	+
	microsepala Urban	*Howard 14598* (IJ)	+
	platantha Britton & Harris ex Moore	*Aiello 1209* (A)	+
		Aiello 1302 (A)	+
Schmidtottia	*elliptica* (Britton) Urban	*Alain 915* (NY)	−
	monantha Urban	*Alain 3442* (NY)	−
	nitens (Britton) Urban	*Shafer 4450* (NY)	−
	parvifolia Alain	*Alain 3592* (NY)	−
	sessilifolia (Britton) Urban	*Alain 3447* (NY)	−
	shaferi (Standley) Urban	*Alain 3298* (NY)	−
	uliginosa (Wernham) Urban	*Shafer 4018* (F)	−
Siemensia	*pendula* (Wright ex Griseb.) Urban	*León 19049* (NY)	−
Thogsennia	*lindeniana* (A. Rich.) Aiello	*Jiménez 4337* (US)	f+
		Ekman 4689 (US)	f+
Portlandia (?)	*guatemalensis* Standley	*Steyermark 48889* (F)	−

Explanation of symbols: (−) negative, (f+) faintly positive, (+) clearly positive.

OTHER ASPECTS OF PORTLANDIA BIOLOGY

ALKALOIDS

Alkaloids have been detected in the leaves, fruit, bark, and other parts of many genera in the Rubiaceae (Willaman & Schubert, 1961; Willaman & Li, 1970; Smolenski *et al.*, 1972, 1974, 1975). Caffeine from the seeds of *Coffea* spp. and quinine from *Cinchona* spp. are familiar examples of alkaloids found in the Rubiaceae. There are only two reports of alkaloids in genera within the Condamineeae (*Pinckneya* and *Pogonopus* (Fong *et al.*, 1972; Willaman & Schubert, 1961)), and none for the genus *Portlandia*, although Raffauf (pers. comm., 1973) obtained a positive test with *P. grandiflora*.

In the present study, dried leaves from herbarium specimens were tested, using the spot method described by Raffauf (1962), for presence or absence of alkaloids (see TABLE 11). This test is capable of detecting alkaloids if present at a concentration of 0.01 percent or higher. No attempt at qualitative analysis was made.

Simple presence or absence of alkaloids, without qualitative analysis, is by itself not a meaningful taxonomic character and should not be used as the determining factor in a taxonomic decision. However, it can add support to decisions made previously on the basis of other characters. In this study, clearly positive results were obtained for only six species: *Cigarrilla mexicana* and all five species of *Portlandia*. Results were faintly positive for the two species of *Cubanola*, *Thogsennia lindeniana*, and *Coutaportla ghiesbreghtiana*. The tests were negative for *Ceuthocarpus*, *Hintonia*, *Isidorea*, *Osa*, *Schmidtottia*, *Siemensia*, and the doubtfully placed *Portlandia guatemalensis*.

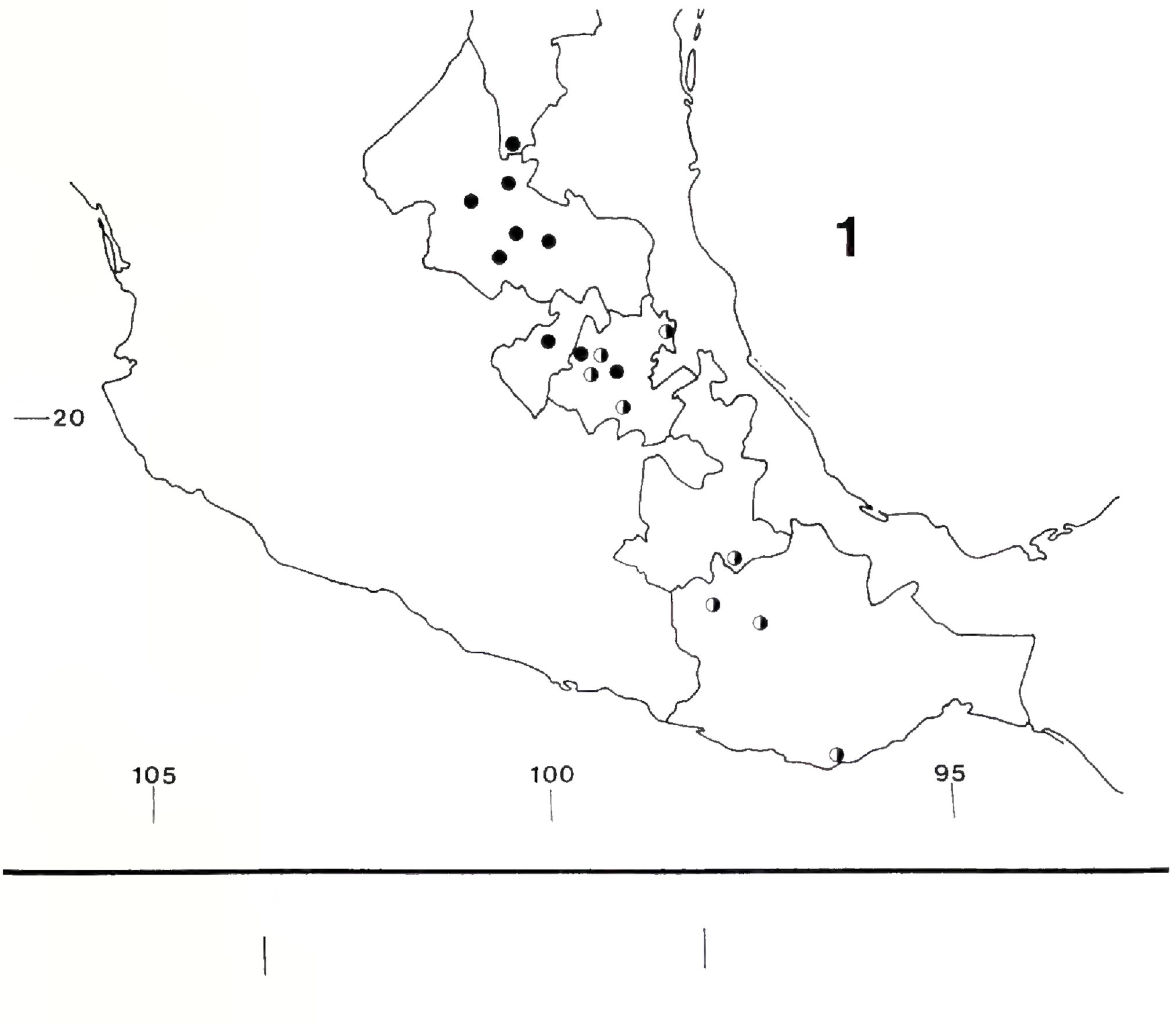
POLLINATION

Among the five species of *Portlandia*, *P. grandiflora* and *P. platantha* have large, white flowers, the odor of which has been described as that of *Gardenia*. *Portlandia harrisii*, with large, pink flowers, is also fragrant. *Portlandia coccinea* and *P. microsepala* have smaller, red, odorless flowers. It seems likely that the white- and pink-flowered, fragrant species are pollinated at night by hawk moths (Sphingidae), and that the red-flowered, odorless species are pollinated during the day by hummingbirds. However, no field observations of *Portlandia* pollination have been reported, and the question of what actually visits these species is still unanswered.

The distributions of the five species of *Portlandia* on Jamaica are shown in MAP 2. It is evident that the red- and pink-flowered species are all located inland, whereas the white-flowered species are found both inland and along the coast. Presumably these distributions are correlated with those of the pollinators, and it would be interesting to know whether similar distribution patterns occur in other plant taxa.

Siemensia, *Coutarea*, *Cigarrilla*, and *Hintonia* have large, white flowers that range in size from 5.6 to 8.7 cm. and are probably pollinated by hawk moths and perhaps also by bees.

Almost certainly the extremely large, white flowers of *Thogsennia*, *Cubanola*, and *Osa*, which range from 18.5 to 27.5 cm. long, are pollinated



MAPS 1, 2. 1, distribution of *Cigarrilla* (solid circles) and *Coutaportla* (circles with right half solid) in Mexico. 2, distribution of five species of *Portlandia* on Jamaica: empty circles = *P. grandiflora*; circles with dot in center = *P. platantha*; circles with lower half solid = *P. harrisii*; circles with right half solid = *P. microsepala*; solid circles = *P. coccinea*.

by moths. Moth-pollination seems especially likely in the case of *Osa*, which has funnelform flowers with a narrow tube 16.5 cm. long.

The remaining genera (*Isidorea*, *Schmidtottia*, *Coutaportla*, and *Ceuthocarpus*) include species with white, pink, red, purple, or yellow flowers ranging in size from 1 to 5 cm. Doubtless a great variety of pollinators, including bees, moths, and hummingbirds, visit these plants.

ASSOCIATED ORGANISMS

During a period of field work in Jamaica, various insects were noted in association with one or more species of *Portlandia*.

The paper wasp, *Polistes crinita* (Hymenoptera - Vespidae, Polistinae), is widespread on the island of Jamaica. It constructs stalked paper nests in bushes, at approximately 1.5 meters above ground level. In St. Catherine Parish, individuals of *Polistes crinita* were observed collecting nectar from the discal nectaries of *Portlandia grandiflora* from which the corollas had fallen. The nectary, which is located around the base of the style, continues to secrete nectar for a day or two after the corolla and style have fallen.

Conotelus is a genus of sap beetles (Coleoptera - Nitidulidae), the adults of which are commonly found in flowers of *Convolvulus sepium* and other members of the Convolvulaceae, where they are known to feed on pollen and nectar (Nishida, 1957). Small numbers of this beetle have been collected in flowers of several other plant families as well, including *Gardenia jasminoides* of the Rubiaceae (Nishida, 1957; Boving & Rozen, 1962). In Jamaica, *Conotelus* was found in the flowers of three species of *Portlandia* (*P. platantha*, *P. harrisii*, and *P. grandiflora*).

Capsules of *Portlandia platantha* and *P. coccinea* brought back to Cambridge from Jamaica contained lepidopteran larvae. These larvae made silken tubes among the seeds in the capsules and fed upon the seeds until pupation. Eclosion of the adults took place two to three months later. The adult moths were identified as members of the Pyralidae, one of the largest and taxonomically most difficult families of the Lepidoptera.

Sugar ants (*Paratrechina longicornis*) were found collecting nectar from fresh flowers of *Portlandia coccinea*.

Specimens of these insects have been deposited in the insect collections of the Museum of Comparative Zoology at Harvard University.

In addition to these field observations, a number of associated organisms were discovered during examination of herbarium specimens.

Several specimens of *Portlandia*, *Cigarrilla*, and *Siemensia* were noted to be covered with scale insects (Homoptera - Coccoidea).

Specimens of *Portlandia* and *Thogsennia* showed damage made by an unidentified leaf miner.

Leaves of *Portlandia grandiflora* from St. Ann Parish, Jamaica, had been attacked by leaf-cutter bees.

The upper leaf surfaces of *Osa pulchra* from Costa Rica were covered

with a number of foliicolous lichens, and a liverwort of the family Lejeuneaceae.

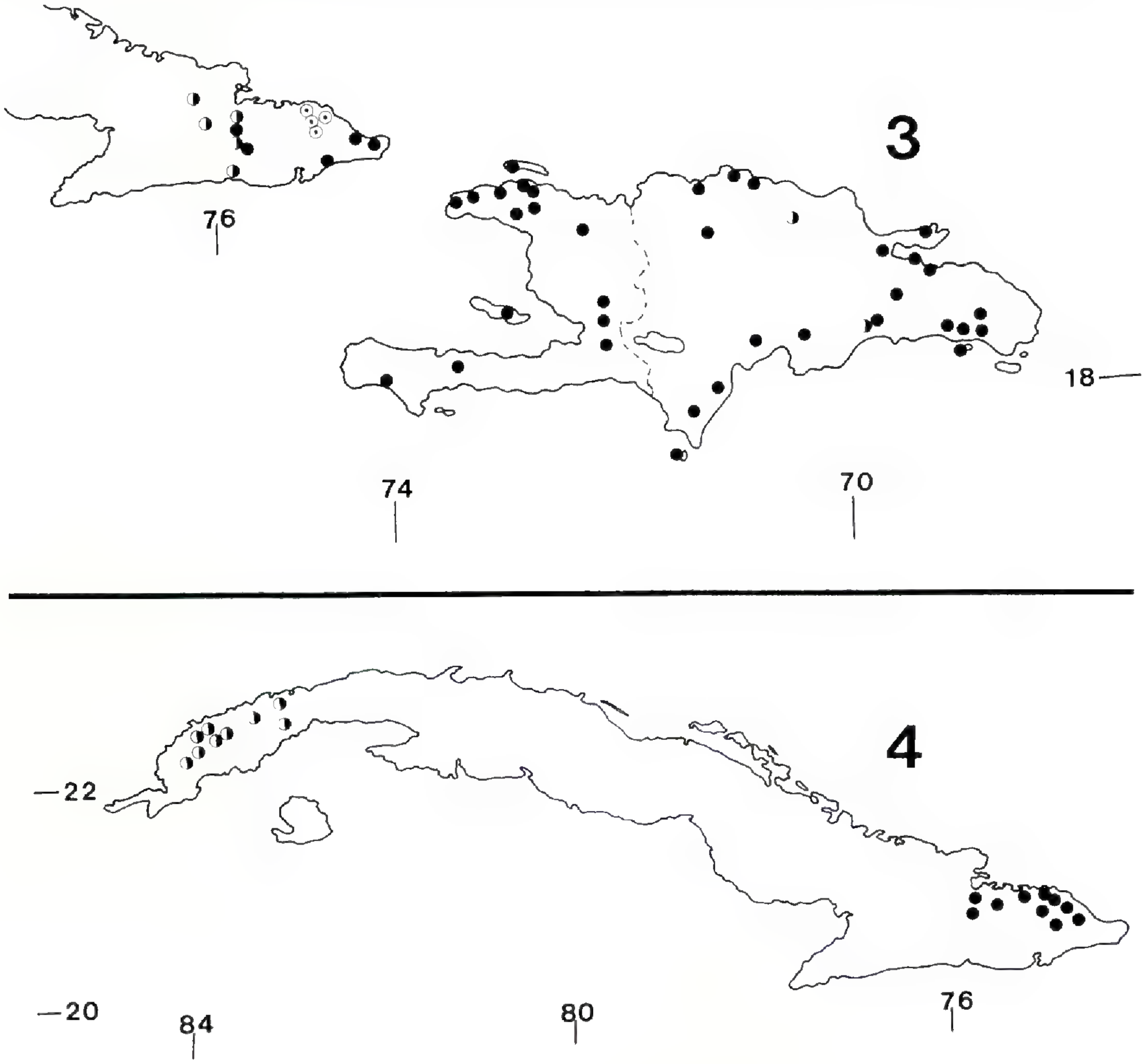
An ascomycete, probably in the family Brefeldiellaceae of the Microthyriales, was found on the upper side of *Cubanola daphnoides* leaves from Cuba.

Atichia millardetii, an ascomycete in the Myriangiales, was found on the upper side of the leaves of *Portlandia grandiflora* from St. Ann Parish, Jamaica.

Distribution

Distributions of the 12 genera under study are described below; those for all genera except *Hintonia*, *Coutarea*, and *Osa* are shown in Maps 1–6.

Portlandia (5 species). Shrubs or small trees up to 6.5 meters tall. Endemic to the island of Jamaica. As shown in Map 2, the red- and pink-



Maps 3, 4. 3, distribution of *Ceuthocarpus* (circles with dot in center), *Isidorea* (solid circles), and *Thogsennia* (circles with right half solid) in Cuba and Hispaniola. 4, distribution of *Schmidtottia* (solid circles) and *Siemensia* (circles with right half solid) in Cuba.

flowered species are found inland, while the white-flowered species are found both inland and along the coast. *Portlandia grandiflora* is under cultivation in southern Florida and on many West Indian islands.

Isidorea (12 species). Shrubs or small trees up to 3 meters tall. Endemic to Hispaniola and eastern Cuba. Each of the species is found on only one of the two islands.

Cubanola (2 species). Shrubs or small trees up to 3 meters tall. One species is endemic to the southeastern portion of the Dominican Republic, the other to eastern and western Cuba.

Thogsennia (1 species). Tree up to 10 meters tall. Endemic to eastern Cuba. Two plants recently found in the Dominican Republic were probably introduced there. Once cultivated in Martinique.

Schmidtottia (10 species). Shrubs or small trees up to 3.5 meters tall. Endemic to eastern Cuba.

Ceuthocarpus (1 species). Shrub up to 4 meters tall. Endemic to eastern Cuba.

Siemensia (1 species). Shrub (often pendent from cliffs) up to 2 meters tall. Endemic to western Cuba.

Cigarrilla (1 species). Shrub or small tree up to 3 meters tall. Endemic to Mexico, where it is found in the states of Hidalgo, Querétaro, San Luis Potosí, and Nuevo León.

Coutaportla (1 species). Shrub up to 2.5 meters tall. Endemic to Mexico, where it is found in the states of Hidalgo, Puebla, and Oaxaca.

Osa (1 species). Tree up to 15 meters tall. Known from two specimens collected on the Osa Peninsula, Costa Rica.

Hintonia (4 species). Shrubs or small trees up to 4 meters tall. Found in western and southern Mexico and into Guatemala. See Bullock (1935) for list of localities.

Coutarea (number of species not certain). Shrubs or small trees up to 15 meters tall. Widespread in tropical America from southern Mexico, through Central America, and into South America.

Cigarrilla, *Coutaportla*, *Cubanola*, *Isidorea*, *Portlandia*, *Siemensia*, and *Thogsennia* grow on limestone, often in arid areas on rugged cliffs or along dry gullies, but also in moister places on wooded hillsides or along streams.

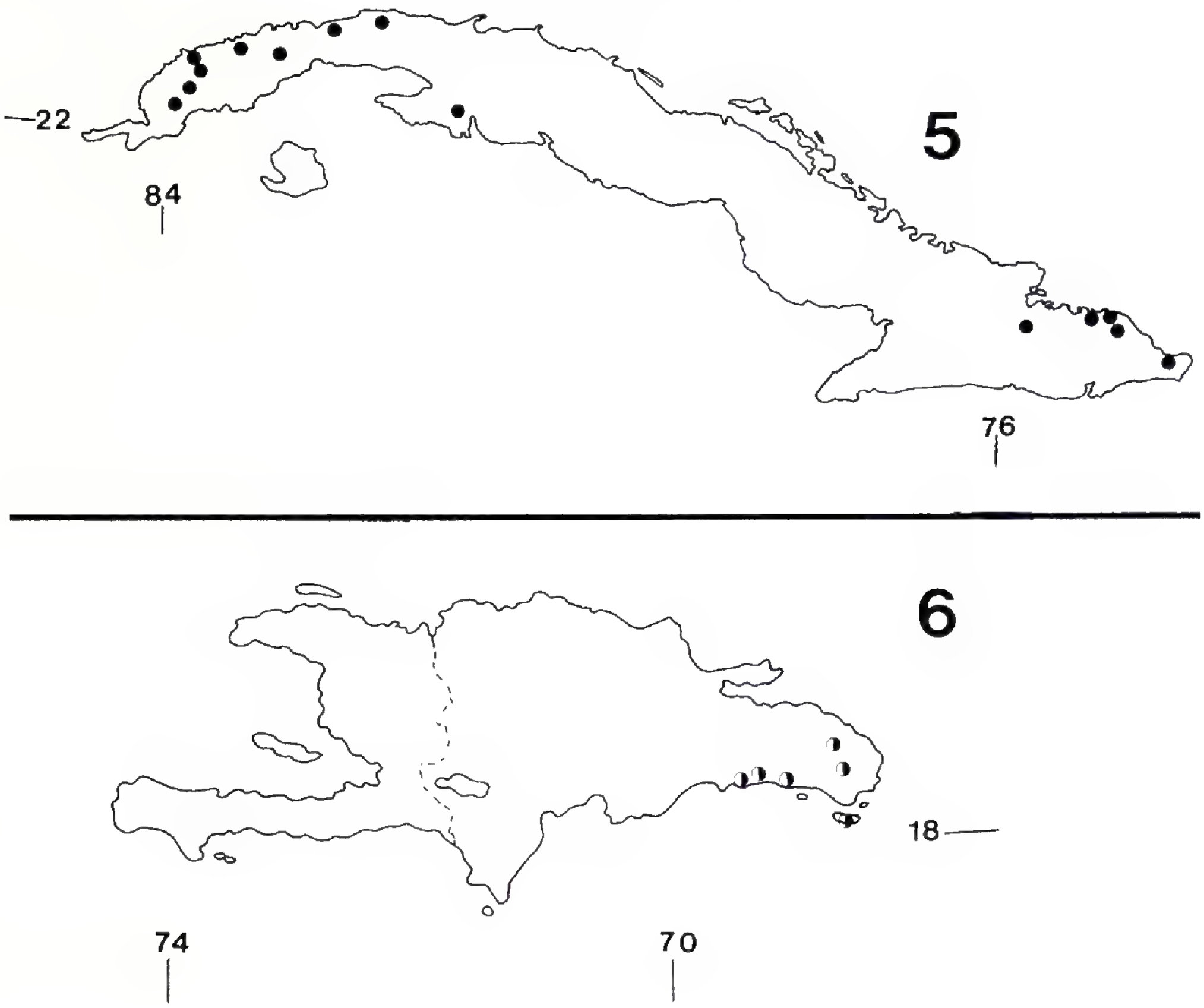
Ceuthocarpus and *Schmidtottia* are found in the serpentine barrens of eastern Cuba.

Osa has been collected from moist forest, but no soil type is mentioned.

Soil data is scanty for *Coutarea* and *Hintonia*. Several labels mention granitic, gravelly, or sandy soil.

PROPAGATION

Portlandia grandiflora was introduced into cultivation in England in 1775 by a Mr. Ellis, Esq. In 1795 William Curtis wrote that, "It forms a very beautiful stove plant, not of difficult growth, and readily disposed to flower. . . ." According to Rees (1819), it was under cultivation in



MAPS 5, 6. 5, distribution of *Cubanola daphnoides* (solid circles) in Cuba. 6, distribution of *C. domingensis* (circles with right half solid) in the Dominican Republic.

the Marchioness of Rockingham's garden at Hillington. An herbarium specimen taken from a flowering plant of *Portlandia grandiflora* in her garden is in the British Museum (Natural History). *Portlandia grandiflora* is found in cultivation in Malaysia and on seven of the West Indian Islands, as well as in England and the United States.

Portlandia coccinea came into cultivation in England in 1812 (Loudon, 1832), as did *P. platantha* in 1850 (Hooker, 1850).

Graham (1841) reported that *Cubanola daphnoides* (under the name *Portlandia daphnoides*) was growing at the Royal Botanic Garden at Edinburgh. He compared the plant to *Portlandia grandiflora* and wrote, ". . . notwithstanding what is said in the Bot. Mag. of the easy culture and free flowering of the *P. grandiflora*, it is universally acknowledged among cultivators that no plant is with greater difficulty kept in good condition, and scarcely any flowers less frequently."

The experience of the Arnold Arboretum in attempting propagation of *Portlandia* has been similar to that of Graham. Although one cutting brought back from Jamaica bloomed within a year, most made little progress in two years. Seeds germinated readily and formed a thick car-

pet of seedlings that subsequently did nothing for months. Gradually most died, although a few managed to add several leaves. Two years later, four or five had attained a height of 20 cm.

By comparison, a specimen of *Portlandia coccinea* grown from seed by Mr. Arthur Sutton outdoors in Jamaica became a flower-bearing shrub almost a meter tall in four years. In addition, several large shrubs of *Portlandia platantha* growing outdoors at the Jennings Estate in Coral Gables, Florida, blossom regularly.

The key to success in propagation of *Portlandia* probably lies in the use of leaf-mold infected with the correct vesicular-arbuscular mycorrhiza, instead of sterilized soil. Vesicular-arbuscular mycorrhizae occur in association with the roots of plants in practically all families of angiosperms. There, in return for simple carbohydrates obtained from the plant, the fungus enables increased ion absorption by the plant roots. While phosphorus is the most important of these ions, passage of nitrogen, potassium, calcium, magnesium, iron, boron, and manganese is also involved. The necessity of this relationship for the normal growth and development of most plants may help explain the success of horticulturists growing *Portlandia* out-of-doors in Jamacia and Florida, and the success of early horticulturists in England who, according to Rees (1819), Hooker (1850), and Bailey (1960), used leaf-mold, and who perhaps received Jamaican soil with their shipments of cuttings.

LOCAL NAMES AND USES

Cigarrilla mexicana. In the state of San Luis Potosí, the colloquial name for *C. mexicana* is "cigarrilla" or "cigarrillo" because the leaves roll up when dry, resembling cigarette paper.

A specimen collected in 1892 in Mineral de Guadalcazar (San Luis Potosí) is labeled "cacaloxochil," an Aztec name meaning "raven-flower, which is white, red, or yellow and very fragrant" (Simeon, 1963).

In the state of Hidalgo, *C. mexicana* is called "flor de San Pedro."

The people of Presa Guadalupe (Hidalgo) place the fresh leaves and twigs of *C. mexicana* in water and boil them. The resulting liquid is swallowed to induce vomiting.

On the 15th day of May, in Santa Catarina (Hidalgo), the flowers of *C. mexicana* are collected and tied in bunches to decorate the church for the Feast of San Isidro.

Cubanola daphnoides. In Cuba this plant is known as "clarine" or "clarín de farallon."

Cubanola domingensis. In Santo Domingo the name "campanitas" is applied to a number of plants in the Convolvulaceae, as well as to *C. domingensis*.

Isidorea leptantha and *I. pungens*. "Palo de cruz" is used to refer to a number of unrelated plants, in addition to these two species of *Isidorea*.

Portlandia. On the island of Jamaica, species of *Portlandia* are referred

to as "wild coffee," as are many other plants with opposite, shining, green leaves. No local names or uses could be discovered either from questioning the people or through examination of collection labels. Patrick Browne (1756), in his description of the genus *Portlandia*, gave the Aztec name "tecomaxachil" for *P. grandiflora*. Since it is unlikely that an Aztec name was in use in Jamaica, perhaps it was applied by a worker who thought the plant resembled a Mexican plant he had seen.

Schmidtottia monantha. The Cuban name for this plant is "flor de tres días."

Thogsennia lindeniana. Cuban names applied to this plant are "clarín cimarron" and "clarín del río."

TAXONOMY

Key to Genera Previously Associated with Portlandia Based Largely on Leaf and Flower Characteristics

1. Leaves coriaceous, somewhat thick.
   2. Leaf apex mucronate or pungent.
      3. Leaves oblong, apex mucronate, secondary veins 2 to 7 pairs; stipules triangular, apex acuminate to attenuate; corolla 4.8–7.2 cm. long; short shoots not present. ..... *Cigarrilla*.
      3. Leaves various in outline, apex pungent, secondary veins 10 to 30 pairs closely packed; stipules narrow with long bristle tips; corolla 1.2–4 cm. long; short shoots often present. ..... *Isidorea*.
   2. Leaf apex neither mucronate nor pungent.
      4. Leaves, when dry, dark (dark brown to black) above and lighter (green to brown) below; stipules truncate or erose, sheathing.
         5. Stipules erose; flowers and fruits surrounded at base by leafy bracts. ..... *Ceuthocarpus*.
         5. Stipules truncate; flowers and fruits not surrounded by bracts. ..... *Schmidtottia*.
      4. Leaves, when dry, not strongly bicolorous; stipules triangular, separate or somewhat connate at base but not sheathing.
         6. Leaves elliptic, not shining, 2–3 cm. long, 0.9–1.3 cm. wide, apex acute; corolla 4-merous, 2–2.5 cm. long; fruit compressed. ..... *Coutaportla*.
         6. Leaves various in outline, shining, 6–22 cm. long, 2.5–14 cm. wide, apex acute to acuminate, or rounded to obtuse; corolla 5-merous, 2.9–22 cm. long; fruit not compressed. ..... *Portlandia*.
1. Leaves chartaceous, thin.
   7. Leaves elliptic to elliptic-oblong, 3.5–5.5 cm. long, 1.6–3 cm. wide, maculate; corolla 5-merous, 5.3–5.7 cm. long. ..... *Siemensia*.
   7. Leaves various in outline, 4–19 cm. long, 1.9–6.5 cm. wide, not maculate; corolla 5-, 6-, or 8-merous, (2–)3–27.5 cm. long.
      8. Leaves elliptic, lanceolate, or ovate, 4–10 cm. long, 1.9–5 cm. wide; flowers 5-, 6-, or 8-merous; calyx lobes 0.7–1.5 cm. long; corolla (2–)3–8 cm. long; seeds winged.
         9. Flowers 1 to 3 or more per axil; corolla 5- or 6-merous, gibbous at

base; fruit strongly compressed, dehiscence both loculicidal and septicidal; seeds elliptic, attachment on side. ..... *Coutarea.*

9. Flowers 1 per axil; corolla 6- or 8-merous; corolla not gibbous at base; fruit not strongly compressed, dehiscence septicidal; seeds broadly elliptic, attachment at end. ..... *Hintonia.*

8. Leaves elliptic, elliptic-oblong, elliptic-lanceolate, or ovate, 7–19 cm. long, 3.5–6.5 cm. wide; flowers 5-merous; calyx lobes 2–2.5 cm. long; corolla 17.8–27.5 cm. long; seeds not winged.

10. Leaves, when dry, usually pale green, secondary veins 4 to 5 pairs; fruits winged; calyx lobes keeled. ..... *Cubanola.*

10. Leaves, when dry, dark green or brown to almost black, secondary veins 6 to 7 pairs; fruits not winged; calyx lobes not keeled.

11. Leaves elliptic or narrowly oblong, apex attenuate; corolla trumpet shaped; fruit dehiscent. ..... *Osa.*

11. Leaves elliptic-lanceolate or oblong-lanceolate, apex acute to acuminate; corolla narrowly funnelform; fruit indehiscent. ..... *Thogsennia.*

KEY TO GENERA PREVIOUSLY ASSOCIATED WITH PORTLANDIA BASED ON CHARACTERISTICS OF FRUITS WITH SEEDS IN PLACE

1. Capsule subtended by overlapping foliaceous bracts. ..... *Ceuthocarpus.*

1. Capsule without bracts.

2. Fruit indehiscent, terete, with no apparent ribs; placentae (in cross section) twice forked. ..... *Thogsennia.*

2. Fruit dehiscent, usually ribbed (often obscurely so) or winged; placentae (in cross section) not forked.

3. Seeds distinctly winged.

4. Capsule greatly flattened perpendicular to the septum; placentae small in cross section; seeds elliptic, attachment at side, 0.8–1.2 cm. long including wing, vertical, perpendicular to septum and placenta, parallel to one another. ..... *Coutarea.*

4. Capsule not flattened; placentae very large and spongy in cross section; seeds broadly elliptic, attachment at end, 0.6–0.7 cm. long including wing, basipetally imbricate. ..... *Hintonia.*

3. Seeds not winged.

5. Funicle or piece of placenta persistent on seeds.

6. Seeds 5–7 mm. long, oriented broadside toward the septum, 8 to 10 per locule; capsule septicidal. ..... *Osa.*

6. Seeds 1.5–3.5 mm. long, perpendicular to the septum, many per locule; capsule strongly loculicidal.

7. Sepals leafy; capsule broadly ribbed, obscurely angled, or smooth, dark brown to black at time of dehiscence. ..... *Portlandia.*

7. Sepals narrow, somewhat keeled; capsule with narrow ribs or smooth, beige to brown. ..... *Isidorea.*

5. Funicle not persistent.

8. Placentae filling middle portion of each locule and tending to divide locule into upper and lower portions; seeds flattened, vertical, perpendicular to septum, arranged with flat sides together in two rows, one row suspended from placenta and lo-

cated in lower portion of locule, the other erect on placenta and located in upper portion of locule.

9. Capsule distinctly flattened perpendicular to the septum; seeds 4 to 6 per locule; dehiscence almost equally loculicidal and septicidal. ..... *Coutaportla.*
9. Capsule not especially flattened; seeds 10 to 16 per locule; dehiscence strongly septicidal, with some loculicidal splitting. ..... *Schmidtottia.*

8. Placentae and seeds not so arranged.
   10. Seeds tiny, 1 mm. or less across; capsule small, 1 cm. long. ..... *Siemensia.*
   10. Seeds 2.5–3.5 mm. long; capsules 2–6 cm. long.
      11. Seeds horizontal; capsule winged; dehiscence loculicidal and septicidal, confined mostly to the disc area of the fruit. ..... *Cubanola.*
      11. Seeds acropetally imbricate; capsule not winged; dehiscence not confined to the disc area. ... *Cigarrilla.*

Portlandia P. Browne, Hist. Jamaica, 164. *t. 11.* 1756. TYPE SPECIES: *Portlandia grandiflora* L.

Shrubs or small trees of limestone areas, up to 6.5 meters high; all parts glabrous. Leaves sessile or with petioles up to 1 cm. long; blades entire, coriaceous, shiny, venation brochidodromous; stipules interpetiolar, widely triangular, acute at apex, somewhat connate at base, with colleters on adaxial side. Inflorescences 1- to 6-flowered, reduced cymes in upper leaf axils, perfect, homostylous, regular, 5-merous, fragrant in white- and pink-flowered species. Calyx lobes subulate to elliptic, often leafy, with colleters on the adaxial surface in some species. Corolla funnelform to broadly funnelform or narrowly campanulate, white, pink, or red, aestivation imbricate. Stamens connate for basal 1–3 mm., adnate to basal 1–3 mm. of corolla, reaching to sinuses of corolla lobes, the filaments pubescent for basal 1.2–6.3 cm., glabrous above. Pollen tricolporate, diffusely foveolate, bearing echinate processes. Ovary 2- (rarely 3-)loculate, turbinate, the placentae linear, adnate to septum nearly its full length, the ovules anatropous, ca. 150 per locule; style glabrous, approximately same length as stamens, the stigmatic area of 2 (rarely 3) lines of papillae, slightly twisted around apical 0.7–6.2 cm. of style. Fruit a capsule opening loculicidally from above. Seeds perpendicular to septum, compressed and angulate due to packing, elliptic to obovate in outline, 2.5–3.5 mm. long, testa tuberculate; funicle persistent; embryo approximately 1.6 mm. long, in center of abundant endosperm.

Five species endemic to the island of Jamaica.

The plant genus *Portlandia* is closely allied to *Isidorea*. In both genera the fruit is a loculicidal capsule, and the horizontal seeds have a tuberculate testa and a persistent funicle. *Portlandia* differs from *Isidorea* in that its larger, flexible, coriaceous leaves are not pungent and have few (6 to 8 pairs) secondary veins; its stipules are widely triangular, not splitting; its twigs are not grooved; and no short shoots are present. As with *Cigarrilla*,

alkaloid tests on leaf material produced strongly positive results in all species of *Portlandia*.

S. Moore (1930) discussed the discrepancy among authors with respect to the style in *Portlandia*. The style has been depicted by various authors as bifid, trifid, or entire. Examination of flowers on herbarium specimens indicate that the stigmatic area consists of 2 (rarely 3 in *P. grandiflora*) lines of papillae slightly twisted around the apex of the style. Whether the style eventually splits into 2 (or 3) arms is a question to be answered, as Moore suggests, in field investigations.

KEY TO THE SPECIES OF PORTLANDIA

1. Corolla red, odorless, 2.5–8.5 cm. long, without a true limb; calyx lobes 0.1–2.5 cm. long, 0.5–5 mm. wide.
   2. Calyx lobes 1–9 mm. long, 0.5–1 mm. wide. ..... *P. microsepala.*
   2. Calyx lobes 9–25 mm. long, 2–6 mm. wide. ..... *P. coccinea.*
1. Corolla white or pink, fragrant, 3.5–22.5 cm. long, flaring near apex to form limb; calyx lobes 0.7–3.6 cm. long, 2–18 mm. wide.
   3. Corolla pink, 5–8.5 cm. long; flowers clustered in uppermost axils; leaves subsessile, oval to orbicular, apex obtuse, base cordate. ..... *P. harrisii.*
   3. Corolla white, often streaked with pink, 3.5–22.5 cm. long; flowers 1 or 2 (or 3) per axil; leaves petiolate, elliptic to ovate, apex acute, base cuneate to rounded.
      4. Flowers large, 10–22.5 cm. long; calyx lobes elliptic, leafy, 1.4–3.6 cm. long, 3–18 mm. wide; capsule ribbed. ..... *P. grandiflora.*
      4. Flowers 3.5–9.9 cm. long; calyx lobes lanceolate to linear-lanceolate, not leafy, 0.7–2.3 cm. long, 2–7 mm. wide; capsule rounded or obscurely angled. ..... *P. platantha.*

Portlandia grandiflora L. Syst. Nat. ed. 10. 1: 928. 1759. TYPE: P. Browne, Hist. Jamaica, *t. 11.* 1756, cited by Linnaeus.

Portlandia grandiflora L. var. *parviflora* S. Moore, Jour. Bot. London **68**: 108. 1930. TYPE: Jamaica, without further locality, *Broughton s.n.* (BRIST, *n.v.*).

Shrub or small tree up to 6.5 meters high. Leaves with petioles 0.5–1 cm. long; blades elliptic, 7.6–22 cm. long, 4.4–13 cm. wide, acute at apex, acute to obtuse at base. Inflorescences reduced cymes in upper leaf axils; flowers 1 (or 2) per cyme, fragrant. Calyx lobes elliptic, often leafy, 1.4–3.6 cm. long, 0.3–1.8 cm. wide; colleters present on adaxial surface. Corolla funnelform to broadly funnelform, 10–22 cm. long, white, sometimes tinged with pink on angles, lobes 2.3–3 cm. long. Filaments pubescent for basal 3–6.3 cm. Stigmatic area 3–6.2 cm. long. Fruit ellipsoid to obovoid, 2–3 cm. long.

DISTRIBUTION. Jamaica, both inland and along the coast in the parishes of Hanover, Westmorland, Trelawny, St. Elizabeth, Manchester, St. Ann, Clarendon, St. Catherine, St. Mary, and St. Andrew.

SPECIMENS EXAMINED. **Jamaica.** Without further locality: *Armstrong s.n.* (E), *Macfadyen s.n.* (K), *Rohr s.n.* (P), *Schumacher s.n.* (S), *Shakespear s.n.* (BM, S),

Swartz s.n. (S), *Wall* in 1930 (S). HANOVER: Campbellton Hill, Logwood, *Adams 8653* (UCWI); near Bull Bay, *Proctor 23471* (A, IJ, TEX); near mouth of Great River, *Proctor 16657* (A, IJ); w. of Lucea, *Adams 13213* (UCWI), *Webster et al. 8568* (GH, IJ, MICH, S, US); Lucea to Montego Bay, *Britton 2916* (F, NY); Green Island to Fish River, *Britton & Hollick 2162* (F, NY, US); Green Island to Orange Bay, *Adams 12770* (UCWI); near North Negril Point, *Proctor 23476* (A, IJ, MICH, TEX); Dolphin Head, *Proctor 10053* (IJ), *Robbins 2583* (UCWI). WESTMORLAND: Town Head to Bushmouth, *Adams 12036* (UCWI). TRELAWNY: near Stewart Town, *Fawcett* in 1904 (BM, UCWI); Windsor estate, *Proctor 15776* (IJ). ST. ELIZABETH: Wallingford to Jenkins, *Adams 6810* (BM, UCWI); Maggoty, *Fosberg 42897* (NY); Maggoty Falls, *West & Arnold 887* (NY); between Maggoty and Y.S., *Clarkson & Kress 75-473* (GH); Oxford near Troy, *Harris 8662* (A, F, NY, UCWI, US), *9407* (F, NY, UCWI), *Marble 715* (NY); Kaiser mine area s. of Gutters, *Howard & Proctor 13762* (A, IJ, NY, US); nw. of Alligator Pond, *Howard & Proctor 13813* (IJ); Pepper, *Miller 1346* (US); Giddy Hall, *Sangster* in 1936 (BM, NY); Mt. Charles estate, 1 mi. ssw. of Giddy Hall P.O., *Proctor 15442* (IJ, US). MANCHESTER: 3 mi. sse. of Auchtembeddie P.O., *Aiello 1307* (A); 1.5 mi. nw. of Mile Gully P.O., *Proctor 22939* (IJ); Porus, *Lloyd 1019* (F, MO); near mouth of the Alligator Hole River, *Lewis* in 1954 (GH, IJ); between Green Bay and Cuckold Point, *Robertson 9208* (UCWI); Gut River, *Adams 6326* (BM, MO, UCWI); Long Bay, *Cornman* in 1965 (IJ). ST. ANN: Fort Point, Discovery Bay, *Asprey 2162* (UCWI), *Stearn 720* (A, BH, UCWI); 2 mi. e. of Rio Bueno, *Howard & Proctor 15127* (A, IJ), *Proctor 35272* (IJ), *Proctor & Stearn 11479* (IJ). CLARENDON: between Lluidas Vale and Croft Hill, *Fosberg 42710* (NY, US); May Pen to Chapelton, *Aiello et al. 1304* (A), *1305* (A). ST. CATHERINE: Rio Cobre, *Britton 3091* (NY); Bogwalk, *Larter 21* (UCWI), *Yuncker 18614* (UCWI); Bogwalk Rd., 4 mi. from Spanish Town, *Burrowes 13025* (UCWI); Lluidas Vale, *Hunnewell & Griscom 14388* (GH, US); St. Clair property, 1 mi. ese. of Riverhead, *Proctor 8375* (A, IJ); 1 mi. w. of Riverhead, *Proctor 24864* (A, BM, IJ, MICH, NY, TEX, US); 1.3 mi. nnw. of Guanaboa Vale P.O., *Proctor 30365* (IJ, NY, TEX); 2 mi. n. of Guanaboa Vale, middle of Stop and Think, *Aiello 1294* (A). ST. MARY: without further locality, *Purdie* in 1843 (K). ST. ANDREW: Stony Hill, *Harris 5878* (BM, UCWI).

This frequently collected, often-cultivated species is the most widespread of the genus. It is distinguished from other species by its very large, white flowers, leafy calyx, and ribbed capsules.

Plants with the corolla approximately 10 cm. long have been described as *Portlandia grandiflora* var. *parviflora*, but such specimens have been collected in five parishes and seem to represent an extreme of corolla length throughout the range of the species. Since no geographic variation is involved, these specimens do not merit varietal status. Although the Broughton material, upon which this taxon was based, is missing from the Bristol Museum, there is reason to believe that it will soon be restored to its rightful place. Therefore, a neotype has not been designated here.

Portlandia coccinea Swartz, Prodr. 42. 1788.

Shrub up to 3 meters high. Leaves sessile or with petioles up to 5 mm. long; blades ovate to elliptic, or obovate, 6–13 cm. long, 2.5–9.8 cm. wide, acute or obtuse at apex, acuminate to acute, obtuse, or cordate at base.

Inflorescences reduced cymes in upper leaf axils; flowers 1 to 3 per cyme. Calyx lobes elliptic, 0.9–2.5 cm. long, 2–6 mm. wide. Corolla funnelform, 2.9–8 cm. long, red with 5 white lines along the angles on inside, lobes 0.5–1.2 cm. long. Filaments pubescent for basal 12 mm. Stigmatic area 0.7–1.2 cm. long. Fruit ellipsoid to widely obovoid, or subglobose, 1–2.1 cm. long.

KEY TO THE VARIETIES

Leaves ovate to broadly ovate or elliptic, apex acute to obtuse, base cordate to obtuse or acute. ..... *P. coccinea* var. *coccinea*.
Leaves elliptic to obovate, apex acute, base cuneate to attenuate. .....
..... *P. coccinea* var. *proctorii*.

Portlandia coccinea Swartz var. coccinea.

Portlandia coccinea Swartz, Prodr. 42. 1788. TYPE: Jamaica, without further locality, *Swartz s.n.* (lectotype, S!; probable isotype, BM!).
Portlandia coriacea Sprengel, Syst. Veg. 1: 708. 1825 (sphalm.).

Leaves ovate to broadly ovate or elliptic, apex acute to obtuse, base cordate to obtuse or acute.

DISTRIBUTION. Jamaica, inland in the parishes of Westmorland, St. James, Trelawny, St. Elizabeth, and Manchester.

SPECIMENS EXAMINED. **Jamaica.** Without further locality: *Bancroft s.n.* (K), *Harridle s.n.* (GH), *Purdie* in 1844 (GH, K), *Purdie s.n.* (NY), *Swartz s.n.* (BM, F, S). WESTMORLAND: Darliston, *Orcutt 6263* (UC). ST. JAMES: 1 mi. se. of Stonehenge, *Proctor 24713* (GH, IJ, MICH, TEX). TRELAWNY: Ramgoat Cave district, *Howard & Proctor 14400* (A, IJ, US); Sherwood Content, *Proctor 11056* (GH, IJ, NY, TEX); Barbecue Bottom, *Ashton* in 1965 (UCWI), *Plowman 3257* (A), *Powell 708* (IJ, NY), *Webster et al. 8431* (IJ, MICH, S, US); Mango Tree Hill, between Burnt Hill and Spring Garden, *Aiello 1308* (A), *Proctor & Alain 24900* (IJ, NY); Burnt Hill, Spring Garden to Junction, *Adams 6773* (BM, MO, UCWI); Burnt Hill, *Barkley 22J240* (IJ). ST. ELIZABETH: Ipswich, *Harris 12505* (NY, UCWI), *12515* (A, BM, CAS, GH, K, MO, NY, S, UCWI, US). MANCHESTER: 1.5 mi. sw. of Craig Hill P.O., *Proctor 24756* (GH, IJ).

Portlandia coccinea Swartz var. proctorii Aiello, var. nov.

Folia elliptica ad obovata, apice acuta, basi cuneata ad attenuatam.

TYPE: Jamaica. St. Catherine, several mi. n. of Old Harbour, *Proctor 32708* (holotype, IJ!; isotype, TEX!).

DISTRIBUTION. Jamaica, inland in St. Catherine Parish.

SPECIMENS EXAMINED. **Jamaica.** ST. CATHERINE: near Planters Hall, *Adams 10298* (UCWI); 3 mi. n. of Gutters, *Proctor 35237* (IJ); 1.5 mi. w. of Lluidas Vale, *Aiello et al. 1295* (A), *Proctor 28015* (IJ); several mi. n. of Old Harbour, *Aiello et al. 1296* through *1299* (A), *Proctor 32708* (IJ, TEX), *32923* (IJ), *34233*

(IJ), *Webster & Wilson 4872* (A); 3.5 mi. n. of Colbeck, *Aiello 1300* (A), *1301* (A).

This variable species is distinguished from *Portlandia microsepala* by its larger, elliptic calyx lobes, and from the remaining species by its red flowers. Although its leaves and those of *P. harrisii* both have cordate bases, the blades differ in overall shape and size. Within *P. coccinea* there is a great deal of variation in leaf shape and corolla size. Corolla length appears to be mosaic throughout the range of the species, while leaf shape shows geographic variation, with specimens collected in St. Catherine Parish having the leaf base cuneate to attenuate, and those collected throughout the remainder of the range having the leaf base cordate to obtuse or acute. The differences are not sufficient to warrant definition of a new species, but are used to distinguish two varieties.

Portlandia platantha Hooker, Bot. Mag. 76: *t. 4534*. 1850. TYPE: from a plant in cultivation at Kew, *Hooker* in 1850 (holotype, K!).

Portlandia grandiflora var. *latifolia* de Candolle, Prodr. **4**: 405. 1830. TYPE: Jamaica, without locality or collector (holotype, G-DC, Microfiche, IDC 800. 691: II. 1!).

Portlandia albiflora Britton & Harris ex Standley, N. Am. Fl. **32**: 12. 1918. TYPE: Jamaica. St. Andrew, Cane River Valley, *Harris 9637* (holotype, NY!; isotypes, A!, BM!, NY!, UCWI!, US!).

Portlandia latifolia Britton & Harris ex S. Moore, Jour. Bot. London **68**: 108. 1930. TYPE: Jamaica. St. Andrew, Hall's Delight, *Harris 12669* (holotype, BM, not seen; isotypes, DS!, F!, GH!, K!, MO!, NY!, P!, UCWI!, US!).

Shrub or small tree up to 5 meters high. Leaves with petioles 2–6 mm. long; blades narrowly to widely elliptic or ovate, 8.2–20.6 cm. long, 2.7–13.1 cm. wide, acute to acuminate or obtuse at apex, attenuate to acuminate or acute at base. Inflorescences reduced cymes in upper leaf axils; flowers 1 to 3 per cyme. Calyx lobes linear-lanceolate or narrowly elliptic, 0.7–2.3 cm. long, 2–7 mm. wide. Corolla broadly funnelform, 3.9–9.9 cm. long, white, often tinged with pink on angles, lobes 1–1.5 cm. long. Filaments pubescent for basal 1.3–2.3 cm. Stigmatic area 0.7–1.3 cm. long. Fruit ellipsoid to widely obovoid or globose, 1–2.1 cm. long.

DISTRIBUTION. Jamaica, coastal areas in the parishes of St. Ann, St. Mary, Kingston, St. Andrew, Portland, and St. Thomas.

SPECIMENS EXAMINED. **Jamaica.** Without further locality: *Burns* in 1949 (UCWI), *Grabham* in 1900 (F, NY), *Hooker* in 1850 (K), *Robins* in 1775 (BM). ST. ANN: Ocho Rios, Hibiscus Lodge, *Proctor 15536* (GH, IJ); Prospect, *Hunnewell 18868* (IJ). ST. MARY: Rio Nuevo, *Hunnewell 15363* (GH); Boscobel, *Adams 9914* (BM, UCWI); Golden Head Beach Hotel, *Aiello 1302* (A); Gibralter [Gibraltar] Beach, near Oracabessa, *Proctor 7456* (A, IJ); Cabarita Island, off Port Maria, *Proctor 7551* (IJ). KINGSTON/ST. ANDREW: Hall's Delight, *Harris 5598* (UCWI), *12669* (DS, F, GH, K, MO, NY, P, UCWI, US); Wareka Hill, *Stewart* in 1965 (UCWI); road to Wareka, *Harris 8922* (A, NY, UCWI), *Maxon 10527* (GH, S, US), *Pelton* in 1956 (IJ), *Webster 13662* (GH, IJ); Long Mountain, *Adams*

6192 (UCWI), *Britton 812* (NY), *Burrowes 13061* (UCWI), *Campbell 6174* (UCWI), *Harris 7870* (F, NY, UCWI), *12530* (BM, CAS, GH, MO, NY, S, UCWI, US), *Proctor 29165* (IJ, NY, TEX), *Robbins 2581* (UCWI), *2582* (UCWI), *Skelding 2676* (UCWI), *Stearn 833* (A, BM), *Weaver 916* (UCWI), *Webster et al. 8369* (BM, F, GH, IJ, MICH, S, US), *Yuncker 17321* (MICH, S); Cane River Valley, *Adams 6961* (BM, UCWI), *Crosby et al. 322* (F, GH, MICH, MO, NY, TEX, UC, US), *duQuesnay 869* (UCWI), *Harris 9637* (A, BM, NY, UCWI, US), *12532* (A, BM, CAS, GH, MO, NY, S, UCWI, US), *12670* (BM, DS, F, GH, K, NY, S, UCWI, US); Lindo's Gap Road, 1.9 mi. from Horse River, *Aiello et al. 1289* (A), *1290* (A). PORTLAND: near Hope Bay, *Harris 6060* (F, NY, UCWI); near mouth of the Rio Grande, *Proctor 11856* (A, IJ), *24885* (IJ, MICH, TEX). ST. THOMAS: Yallah's Point, *Britton 3671* (NY); 0.5 mi. w. of White Horses, *Aiello et al. 1291* through *1293* (A), *Proctor 23058* (BM, GH, IJ, MICH, NY, TEX); 2 mi. inland from Rozelle, *Adams 13035* (BM, UCWI); w. of Morant Bay, *Chrysler 4638* (F).

This highly variable species is similar to *Portlandia grandiflora*, but the flowers are smaller, the calyx is not leafy, and the capsules are not ribbed.

Portlandia platantha is the most variable species of the genus and has been known under the names *P. albiflora* and *P. latifolia*, the original epithet being ignored in the literature. FIGURE 91 (map) shows the localities from which specimens named as these two species have been collected. Upon describing *P. latifolia*, Britton and Harris distinguished it from *P. albiflora* by its "broader leaves rounded (not cuneate) at base and the calyx with longer and markedly broader lobes." There are two main problems with this distinction. First, specimens (*Webster 8369* (MICH, S)) collected at the type locality for *P. latifolia* bear both leaf types. Second, when leaf base angle is plotted against leaf width for specimens from all known localities (FIGURE 91), there is a great deal of overlap, and no clear distinction can be demonstrated among populations, although there is a tendency for the leaves of plants along the northern coast to be larger and broader than those of plants along the southern coast. In addition, since corolla length varies from 5.6 to 8.5 cm. for plants labeled *P. albiflora*, and from 3.9 to 9.9 cm. for plants labeled *P. latifolia*, it is not a distinguishing character. There is no choice but to include both *P. albiflora* and *P. latifolia* under the earliest name available, *P. platantha*. While the type locality for *P. platantha* in nature is not recorded, specimens collected at the Golden Head Beach Hotel in St. Mary Parish closely resemble Hooker's specimen in details of leaf size and shape, and corolla size and shape.

Portlandia harrisii Britton, Bull. Torrey Bot. Club 39: 8. 1912. TYPE: Jamaica. Clarendon, Peckham Woods, *Harris 10975* (holotype, NY!; isotypes, NY!, UCWI!, US!).

Shrub or small tree up to 6 meters high. Leaves sessile; blades widely elliptic to circular, 6–14.2 cm. long, 5.7–14 cm. wide, rounded at apex, cordate at base. Inflorescences reduced cymes in upper leaf axils; flowers 3 to 6 per cyme, fragrant. Calyx lobes elliptic, 1.4–2.5 cm. long, 4–5 mm. wide; colleters present on adaxial surface. Corolla narrowly campanulate, 5–8 cm. long, pink, lobes 1.5–2 cm. long. Filaments pubescent for basal

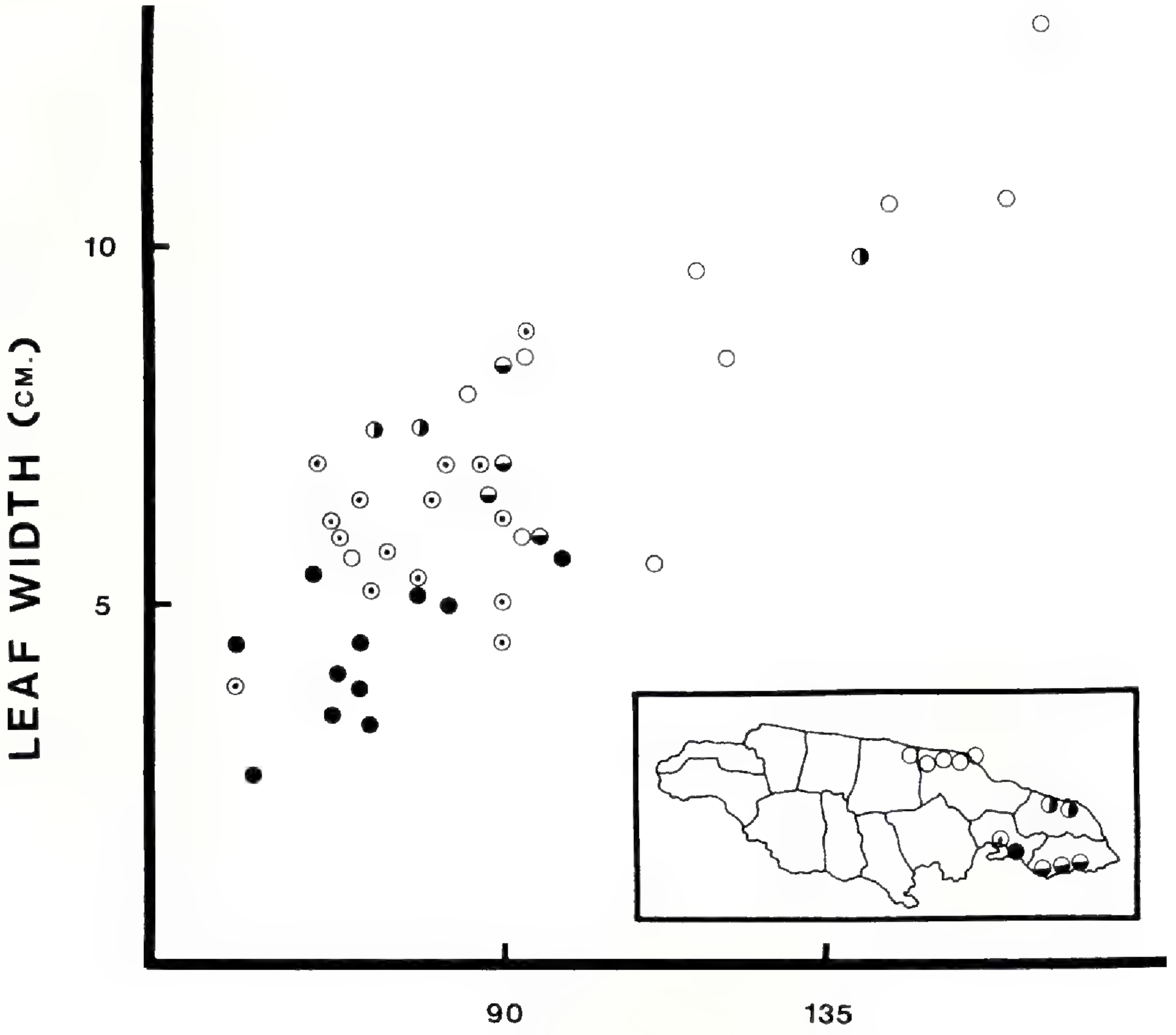


FIGURE 91. Plot of leaf base angle against leaf width for specimens of *Portlandia platantha* from all known localities. Circles with dot in center = type locality for *P. latifolia*; solid circles = type locality for *P. albiflora*; remaining symbols = localities for other specimens labeled *P. latifolia*.

1.7–2.6 cm. Stigmatic area 2–3 cm. long. Fruit ellipsoid to widely obovoid, sometimes subglobose, or rarely ovoid, 1.7–2.5 cm. long.

DISTRIBUTION. Jamaica, inland in the parishes of Clarendon and St. Ann.

SPECIMENS EXAMINED. **Jamaica.** CLARENDON: Aenon Town to McKoy, *Adams 11039* (MO, UCWI); Peckham Woods, *Aiello 1306* (A), *Harris 10975* (NY, UCWI, US), *11046* (NY, UCWI, US), *11209* (F, NY, UCWI, US), *12789* (F, NY, UCWI, US), *Proctor 9781* (A, IJ, NY), *10227* (A, IJ). ST. ANN: Norwood to Bailey, *Adams 12488* (BM, UCWI); Douglas Castle district, *Proctor 26725* (GH, IJ).

This species, known from four localities, differs from the others in its sessile, broadly elliptic to orbicular leaves with cordate bases; its inflorescences of 3 to 6 flowers per axil; and its pink, narrowly bell-shaped corolla.

Portlandia microsepala Urban, Repert. Sp. Nov. **13**: 478. 1915. TYPE: Jamaica. St. Ann, Albion, *Alexander* in 1850 (holotype, K!).

Shrub or small tree up to 3 meters high. Leaves with petioles 5–8 mm. long; blades ovate to elliptic, 8.2–14.4 cm. long, 4.3–8 cm. wide, acute or short-acuminate at apex, acute or obtuse at base. Flowers solitary in upper leaf axils. Calyx lobes subulate, 2–9 mm. long, 0.5–1 mm. wide. Corolla funnelform, 5.5–6.7 cm. long, red, lobes 5 mm. long. Filaments pubescent for basal 1.2–1.4 cm. Stigmatic area 0.8–1 cm. long. Fruit ellipsoid to widely obovoid, 1.6–2 cm. long.

DISTRIBUTION. Jamaica, inland in St. Ann Parish.

SPECIMENS EXAMINED. **Jamaica.** Without further locality: *Alexander* in 1850 (NY, P). ST. ANN: Linton property near Claremont, *Aiello et al. 1303* (A), *Howard et al. 14598* (A, IJ); Ramble estate, 2 mi. sw. of Claremont, *Proctor 9329* (IJ); Albion, *Alexander* in 1850 (K); 8.5 mi. w. of Albion, *Hespenheide et al. 1035* (GH, MO, UC, US); Union, Moneague, *Sturridge* in 1887 (K).

This rare species, known from four localities, has been collected in flower only three times. It is distinguished from the others by its very small, subulate calyx lobes. *Portlandia microsepala* and *P. grandiflora* have longer petioles than do the remaining three species.

NAMES EXCLUDED FROM PORTLANDIA OR REDUCED TO SYNONYMY

Portlandia acuminata Willdenow ex Roemer & Schultes, Syst. Veg. **5**: 23. 1819. From the specimen *Bredemeyer* (B-WILLD, Microfiche, IDC 7440. 275: II. 2!), this is a species of **Coutarea** Aublet.

Portlandia albiflora Britton & Harris ex Standley, N. Am. Fl. **32**: 12. 1918 = **Portlandia platantha** Hooker, Bot. Mag. **76**: *t. 4534*. 1850.

Portlandia brachycarpa Urban, Symb. Antill. **9**: 135. 1923 = **Isidorea brachycarpa** (Urban) Aiello.

Portlandia coriacea Sprengel, Syst. Veg. **1**: 708. 1825 (sphalm.) = **Portlandia coccinea** Swartz, Prodr. 42. 1788.

Portlandia corymbosa Ruiz & Pavon, Fl. Peruv. **2**: 49. 1799 = **Exostema corymbosum** Sprengel, Syst. Veg. **1**: 706. 1825.

Portlandia daphnoides R. Graham, Edinb. New Philos. Jour. **30**: 206. 1840–41 = **Cubanola daphnoides** (R. Graham) Aiello.

Portlandia domingensis Britton, Bull. Torrey Bot. Club **41**: 24. 1914 = **Cubanola domingensis** (Britton) Aiello.

Portlandia elliptica Britton, *ibid.* 22 = **Schmidtottia elliptica** (Britton) Urban, Symb. Antill. **9**: 139. 1923.

Portlandia ghiesbreghtiana Baillon, Adansonia **12**: 300. 1879 = **Coutaportla ghiesbreghtiana** (Baillon) Urban, Symb. Antill. **9**: 147. 1923.

Portlandia grandiflora Zuccagni in Roemer, Collect. 129. 1806 = **Solandra grandiflora** Swartz, Sv. Vet.-akad. Handl. **8**: 300. *t. 11*. 1787.

Portlandia grandiflora var. *latifolia* DC. Prodr. **4**: 405. 1830 = **Portlandia platantha** Hooker, Bot. Mag. **76**: *t. 4534*. 1850.

Portlandia grandiflora var. *parviflora* S. Moore, Jour. Bot. London **68**: 108. 1930 = **Portlandia grandiflora** L. Syst. Nat. ed. 10. **1**: 928. 1759.

Portlandia guatemalensis Standley, Jour. Wash. Acad. **18:** 162. 1928. Until mature fruit seen, cannot be assigned to any genus.

Portlandia gypsophylla Macfadyen, Fl. Jamaica **2:** 216. 1837 (*nomen illegit.*, Art. 63, ICBN) = **Thogsennia lindeniana** (A. Richard) Aiello.

Portlandia gypsophila Macfadyen ex Grisebach, Fl. Brit. W. Indian Is. 324. 1861 = **Thogsennia lindeniana** (A. Richard) Aiello.

Portlandia hexandra Jacquin, Enum. Pl. Carib. 16. 1760 = **Coutarea hexandra** (Jacquin) Schumann in Martius, Fl. Brasil. **6**(6): 196. 1889.

Portlandia hexandra L. Mant. Pl. ed. *2*. 45. 1767 = **Coutarea hexandra** (Jacquin) Schumann in Martius, Fl. Brasil. **6**(6): 196. 1889.

Portlandia hexandra (L.) ex Vellozo, Quinogr. Portug. 161. *t. 9*. 1799 = **Coutarea hexandra** (Jacquin) Schumann in Martius, Fl. Brasil. **6**(6): 196. 1889.

Portlandia hexandra Vellozo (non Jacquin) ex Steudel, Nomencl. ed. *2*. **1:** 429. 1840. Vellozo cites Gmelin, Syst. Nat. ed. 13a. 1796, which in turn cites Jacquin, Select. Stirp. Am. Hist. *t. 65* (ca. 1780) = **Coutarea hexandra** (Jacquin) Schumann in Martius, Fl. Brasil. **6**(6): 196. 1889.

Portlandia involucrata Wernham, Jour. Bot. London **51:** 320. 1913 = **Ceuthocarpus involucratus** (Wernham) Aiello.

Portlandia latifolia Britton & Harris ex S. Moore, Jour. Bot. London **68:** 108. 1930 = **Portlandia platantha** Hooker, Bot. Mag. **76:** *t. 4534*. 1850.

Portlandia lindeniana (A. Richard) Britton, Bull. Torrey Bot. Club **41:** 23. 1914 = **Thogsennia lindeniana** (A. Richard) Aiello.

Portlandia longiflora Meissner ex Grisebach, Cat. Pl. Cubens. 126. 1866 = **Cubanola daphnoides** (R. Graham) Aiello.

Portlandia lumaeana (Baillon) Baillon, Hist. Pl. **7:** 333. 1880 = **Hintonia lumaeana** (Baillon) Bullock in Hooker's Ic. Pl. **33:** 5. 1935.

Portlandia mexicana (Zuccarini & Martius) Hemsley, Diagn. Pl. Nov. 31. 1879 = **Cigarrilla mexicana** (Zucc. & Martius ex DC.) Aiello.

Portlandia nitens Britton, Bull. Torrey Bot. Club **39:** 10. 1912 = **Schmidtottia nitens** (Britton) Urban, Symb. Antill. **9:** 141. 1923.

Portlandia oblanceolata Urban, *ibid.* 136 = **Isidorea oblanceolata** (Urban) Aiello.

Portlandia pendula Wright ex Grisebach, Cat. Pl. Cubens. 126. 1866 = **Siemensia pendula** (Wright) Urban, Symb. Antill. **9:** 145. 1923.

Portlandia polyneura Urban, *ibid.* 135 = **Isidorea polyneura** (Urban) Aiello.

Portlandia pterosperma S. Watson, Proc. Am. Acad. **24:** 52. 1889 = **Hintonia latiflora** (Sessé & Moç. ex DC.) Bullock in Hooker's Ic. Pl. **33:** 4. *t. 3295*. 1935.

Portlandia sessilifolia Britton, Bull. Torrey Bot. Club **41:** 21. 1914 = **Schmidtottia sessilifolia** (Britton) Urban, Symb. Antill. **9:** 142. 1923.

Portlandia shaferi Standley, N. Am. Fl. **32:** 9. 1918 = **Schmidtottia sessilifolia** (Britton) Urban subsp. **shaferi** (Standley) Borhidi, Bot. Közlem. **58:** 176. 1971.

Portlandia speciosa Baillon, Hist. Pl. **7:** 381. 1879 = **Coutarea hexandra** (Jacquin) Schumann in Martius, Fl. Brasil. **6**(6): 196. 1889.

Portlandia tetrandra L. f. Suppl. Pl. 143. 1781 = **Bikkia tetrandra** (L. f.) A. Richard, Mém. Fam. Rub. 151. 1830.

Portlandia tetrandra Forster f. Prodr. 15. 1786 = **Bikkia tetrandra** (L. f.) A. Richard, Mém. Fam. Rub. 151. 1830.

Portlandia uliginosa Wernham, Jour. Bot. London **51:** 320. 1913 = **Schmidtottia uliginosa** (Wernham) Urban, Symb. Antill. **9:** 139. 1923.

Ceuthocarpus Aiello, gen. nov.

Differt a *Schmidtottia*: floribus terminalibus et solitariis, ad basim involucro bractearum foliacearum circumcinctis; staminibus partim exsertis; seminibus ascendentibus imbricatisque.

TYPE SPECIES: *Ceuthocarpus involucratus* (Wernham) Aiello (basionym, *Portlandia involucrata* Wernham, 1913).

Shrubs of serpentine barrens, up to 4 meters high. Leaves 2 or 3 per node; petioles 0.5–1.3 cm. long; blades narrowly elliptic to elliptic-obovate or obovate, rounded at apex, acute to attenuate at base, 2–6 cm. long, 0.6–2.5 cm. wide, entire, coriaceous, dark brown to black above and shiny when dry, lighter brown below, with very sparse unicellular hairs on lower surface, the venation brochidodromous, the 3 to 6 pairs of veins obscure; stipules interpetiolar, connate to form a sheath, erose. Flowers terminal and solitary, perfect, homostylous, regular, 5- or 6-merous, surrounded at base by an involucre of leafy bracts. Calyx lobes linear to subulate, 0.7–1.3 cm. long, 1–2 mm. wide. Corolla funnelform, red, 3–3.5 cm. long, with lobes 0.7–1.1 cm. long. Stamens connate for basal 1–2 mm., adnate to basal 1–2 mm. of corolla, slightly exserted, the filaments pubescent for basal 1 cm., glabrous above. Pollen tricolporate, diffusely foveolate, bearing echinate processes. Ovary 2-loculate, placentae globular, adnate to center of septum, the ovules anatropous, ca. 20 per locule; style approximately same length as stamens. Fruit a capsule opening both loculicidally and septicidally from above, ellipsoid to broadly ellipsoid or globose, 1–1.6 cm. long. Seeds acropetally imbricated, broadly elliptic to obovate in outline, 3–3.3 mm. long, testa reticulate.

One species endemic to eastern Cuba.

Ceuthocarpus is separated from *Schmidtottia* in having seeds that are acropetally imbricated, not some pendulous and some ascending; flowers and fruits that are surrounded at the base by an involucre of leafy bracts, not naked; flowers that are terminal and solitary, not in terminal cymes; and stamens that are somewhat exserted, not included.

Schmidtottia cubensis, with its solitary, terminal flowers and its two or three leaves per node, may belong to *Ceuthocarpus*, but the fruiting material with seeds in place necessary for deciding its placement is not available at this time.

Ceuthocarpus differs from *Portlandia* and the other genera studied in having the flower and fruit surrounded at the base by an involucre of bracts, not naked, and flowers that are terminal and solitary, not axillary or in terminal cymes. It differs from *Portlandia* in several characters: the stamens are somewhat exserted, not included; the fruits have seeds that are acropetally imbricated, not horizontal; and the seeds lack the persistent funicle of *Portlandia* and have a testa that is reticulate, not tuberculate.

The name *Ceuthocarpus* is formed from two Greek roots, *ceutho-* (concealed, hidden) and *carpus* (a fruit), in allusion to the fruit being partially hidden by the leafy involucre.

Ceuthocarpus involucratus (Wernham) Aiello, comb. nov.

Portlandia involucrata Wernham, Jour. Bot. London **51:** 320. 1913. TYPE: Cuba. Oriente, Moa, Camp la Gloria, s. of Sierra Moa, *Shafer 8282* (holotype, NY!; isotypes, F!, GH!, MO!, NY!, US!).

Schmidtottia involucrata (Wernham) Alain, Contr. Ocas. Mus. Hist. Nat. Col. "de la Salle" **17:** 10. 1959.

DISTRIBUTION. Eastern Cuba.

Characters of the genus.

SPECIMENS EXAMINED. **Cuba.** ORIENTE: Camp Toa to Camp la Barga, *Shafer 4138* (NY); near mouth of Río Yamaniguey, *Shafer 4244* (NY); Moa region, Río Yagrumaje se. of Punta Gorda, *Acuña 12769* (US), *Clemente 3614* (NY), *Clemente & Alain 3859* (GH, NY, US), *Webster 3781* (GH, MICH); Moa, near Punta Gorda, *Clemente 4472* (NY); Moa, Camp la Gloria, s. of Sierra Moa, *Shafer 8262* (NY), *8276* (NY, US), *8282* (F, GH, MO, NY, US); Sierra de Moa, *Alain 3340* (NY); Moa, plateau between Río Cabanas and Río Moa, *Victorin & Clément 56723* (US); Moa, Valley of Cayoguán River, *Alain & Clemente 845* (GH, NY), *Clemente 4485* (GH, NY).

Cigarrilla Aiello, gen. nov.

Differt a *Portlandia*: foliis oblongis, in sicco involutis; placentis magnis et spongiosis; capsula dehiscenti et loculicide et septicide; seminibus ascendentibus imbricatisque, colliculosis, et funiculis non persistentibus.

TYPE SPECIES: *Cigarrilla mexicana* (Zucc. & Martius ex DC.) Aiello (basionym, *Coutarea mexicana* Zucc. & Martius ex DC. 1830).

Shrubs or small trees of limestone areas, up to 5 meters high; all parts glabrous. Leaves with petioles 3–5 mm. long; blades oblong, acute and mucronate at apex, obtuse to acute at base, 3.5–6.5 cm. long, 1.6–2 cm. wide, entire, coriaceous, shiny, curling when dry, the venation brochidodromous; stipules interpetiolar, widely triangular, acuminate to attenuate at apex, somewhat connate at base, sometimes splitting from base to apex with age, with colleters on the adaxial surface. Flowers solitary in the upper leaf axils, perfect, homostylous, regular, 5-merous, fragrant. Calyx lobes narrowly triangular to subulate, 5–7 mm. long, 2 mm. wide, with colleters present on the adaxial surface. Corolla broadly funnelform, white, 4.8–7.2 cm. long, with lobes 1.1–1.5 cm. long, aestivation imbricate. Stamens connate for basal 1 mm., adnate to basal 1 mm. of corolla, reaching to sinuses of corolla lobes, the filaments pubescent for basal 1.1 cm., glabrous above. Pollen tricolporate, diffusely foveolate, bearing echinate processes. Ovary 2-loculate, turbinate, the placentae large and spongy, adnate to central portion of septum, the ovules anatropous, ca. 30 per locule; style glabrous, approximately same length as stamens, the stigmatic area of 2 lines of papillae, slightly twisted around apical 2.5 cm. of style. Fruit a capsule opening both loculicidally and septicidally from above, obovoid or oblong-ellipsoid, 1.2–1.8 cm. long. Seeds acropetally

imbricated, compressed, elliptic to ovate in outline, 3–3.4 mm. long, testa colliculate to low tuberculate; embryo approximately 1.9 mm. long, in center of abundant endosperm.

One species endemic to Mexico.

Cigarrilla, while similar to *Portlandia* in the construction of the flowers, the leatheriness of the leaves, the appearance of the capsules, and the presence of alkaloids in the leaves, differs from that genus primarily in having a large, spongy placenta, acropetally imbricate seeds, a colliculate seed coat, and a non-persistent funicle, but also in leaf shape and size, and in the fact that the leaves curl when dry.

Cigarrilla differs from *Coutarea* in having a large, spongy placenta, acropetally imbricated seeds, a colliculate seed coat, leathery leaves, and a radially symmetrical corolla.

Cigarrilla and *Ceuthocarpus* both have acropetally imbricated seeds, but the two genera differ greatly in characters of leaf, stipule, inflorescence, fruit, and seed coat.

Because *Cigarrilla* has imbricated seeds, it cannot belong to the Condamineeae, as that tribe is presently defined, and would probably be better placed in either the Hedyotideae or the Cinchoneae.

"Cigarrilla" is the colloquial name for the plant in the state of San Luis Potosí, Mexico.

Cigarrilla mexicana (Zucc. & Martius ex DC.) Aiello, comb. nov.

Coutarea mexicana Zucc. & Martius ex DC. Prodr. **4**: 350. 1830. TYPE: Mexico, without further locality, *Martius* in 1829 (holotype, G-DC, Microfiche, IDC 800. 680: II. 7!).

Portlandia mexicana (Zucc. & Martius ex DC.) Hemsley, Diagn. Pl. Nov. 31. 1879.

Characters of the genus.

DISTRIBUTION. Endemic to Mexico, where it is found in the states of Hidalgo, Querétaro, San Luis Potosí, and Nuevo León.

SPECIMENS EXAMINED. **Mexico.** Without further locality: *Bates s.n.* (K), *Ehrenberg 998* (US), *Martius 1829* (G-DC). NUEVO LEÓN: Medina, *Karwinsky 307* (F). SAN LUIS POTOSÍ: without further locality, *Virlet d'Aoust 1917* (F, P); Presa de Guadalupe, *Aiello et al. 1225* through *1229* (A), *Medellín et al. 9846* (SLPM); 8 km. sw. of Presa de Guadalupe, *Rzedowski 6749* (BH, ENCB, F, MICH, MO, SLPM, TEX); Charco Blanco, *Aiello et al. 1230* through *1235* (A), *Medellín et al. 9843* (SLPM); Mineral de Guadalcazar, *Villader 12* (MEXU); Mpio. de Guadalcazar, Ejido San Francisco del Tulillo, *Jiménez & Cruz 12297* (A, SLPM); Mpio. de San Nicolás Tolentino, Cruz de Encino, Sierra de Alvarez, *Hidalgo Hernández 12296* (A, SLPM), *de Jesús Olvera 12298* (A, SLPM); 3 km. w. of Santa Catarina, *Aiello et al. 1237* through *1240* (A), *Medellín et al. 9840* (SLPM), *Rzedowski 5725* (ENCB, SLPM, TEX); Las Tablas, *Pennell 18027* (F, GH, MICH, NY, UC); Minas de San Rafael, *Purpus 5042* (F, GH, MO, NY, UC, US), *5205* (E, F, GH, MO, NY, P, UC, US). QUERÉTARO: between Visarón and Higuerillas, *Alta-*

mirano 1676 (US), *Rose et al. 9767* (NY, US). HIDALGO: w. of Zimapán, *Aiello et al. 1203* through *1208* (A), *Coulter 225* (GH, K), *González Quintero 2360* (DS, ENCB, F, MICH, TEX), *Karwinsky* in 1827 (NY), *Miranda 9002* (MEXU), *Moore 5447* (BH, BM, GH, MICH, UC), *Moore & Wood 4381* (A, BH, BM, UC, US); Actopan, *Bravo* in 1936 (F); e. of Metztitlán, Barranca de Salitre, *Aiello et al. 1223* (A), *1224* (A).

Cubanola Aiello, gen. nov.

Differt a *Portlandia*: foliis chartaceis, non nitidis, pallide viridibus; stipulis ad apicem acuminatis usque attenuatis; sepalis longis et angustis; placentis in sectione transversa circularibus; capsula alata, dehiscenti et loculicide et septicide; seminibus reticulatis usque foveatis, funiculis non persistentibus.

TYPE SPECIES: *Cubanola daphnoides* (R. Graham) Aiello (basionym, *Portlandia daphnoides* R. Graham, 1841).

Shrubs or small trees of limestone areas, up to 3 meters high; all parts glabrous. Leaves petiolate; blades entire, chartaceous to slightly coriaceous, dull, light green, the venation brochidodromous; stipules interpetiolar, triangular, acuminate to attenuate at apex, slightly connate at base. Flowers solitary in the upper leaf axils, perfect, homostylous, regular, 5-merous, fragrant. Calyx lobes subulate, with colleters present on the adaxial surface. Corolla narrowly funnelform, white, aestivation imbricate. Stamens connate for basal 1 mm., adnate to basal 1 mm. of corolla, reaching to sinuses of corolla lobes, the filaments pubescent for basal 7 cm., glabrous above. Pollen tricolporate, diffusely foveolate, bearing echinate processes. Ovary 2-loculate, turbinate, the placentae circular in cross section, adnate to septum nearly its full length, the ovules anatropous, several hundred per locule; style glabrous, approximately same length as stamens, the stigmatic area of 2 lines of papillae, slightly twisted around apical 1.4 cm. of style. Fruit a capsule opening both loculicidally and septicidally from above. Seeds perpendicular to septum, compressed and angulate due to packing, elliptic to broadly elliptic in outline, 3.1–3.5 mm. long, testa reticulate to foveate; embryo approximately 1.5 mm. long, in center of abundant endosperm.

Two species, one endemic to eastern and western Cuba, the other to the Dominican Republic.

Cubanola is similar to *Portlandia* in having large flowers, but differs from it in having a placenta that is circular in cross section, a winged, loculicidally and septicidally dehiscent capsule, reticulate to foveate seeds without a persistent funicle, thin, dull, light green leaves, stipules with an acuminate to attenuate apex, and long, narrow calyx lobes.

Cubanola is superficially very similar to *Thogsennia*, which also has long, narrow calyx lobes, large, white flowers, and horizontal seeds, but the latter genus has dark leaves, a placenta that is twice-forked in cross section, a wingless, indehiscent capsule, and collapsed, colliculate seeds.

The name of the genus derives from the fact that one of the two species is endemic to Cuba and the other to Hispaniola.

KEY TO THE SPECIES OF CUBANOLA

Petioles 5–15 mm. long; corolla 19.6–28.7 cm. long, tube 9–12 cm. long, lobes widely triangular, 9–18 mm. long; capsule obovoid, truncate at apex, fruiting pedicels, 2–2.5 cm. long. ..... *C. daphnoides.*

Petioles 1–3 mm. long; corolla 18.5–19.8 cm. long, tube 6.5–7 cm. long, lobes very shallowly triangular, 7–8 mm. long; capsule ellipsoid, obtuse at apex, fruiting pedicels 1.4–1.7 cm. long. ..... *C. domingensis.*

Cubanola daphnoides (R. Graham) Aiello, comb. nov.

Portlandia daphnoides R. Graham, Edinb. New Philos. Jour. **30:** 206. 1841. NEOTYPE: Cuba. Matanzas, Yumury Valley, near Matanzas, *Rugel 374* (NY!).

Gonianthes sagraeana A. Richard in Sagra, Hist. Cuba **11:** 10. 1850. TYPE: Cuba, without further locality, *Sagra s.n.* (holotype, P!).

Portlandia longiflora Meissner ex Grisebach, Cat. Pl. Cuba, 126. 1866. TYPE: Cuba. Matanzas, Yumury Valley, near Matanzas, *Rugel 374* (lectotype, NY!).

Shrub or small tree up to 3 meters high. Leaves with petioles 0.5–1.5 cm. long; blades elliptic, elliptic-oblong, or obovate, 9.5–18 cm. long, 2.5–8.8 cm. wide, acute or acuminate at apex, acuminate or acute at base. Calyx lobes 2–3.2 cm. long, 1–2 mm. wide. Corolla 17.8–28.7 cm. long, tube 6.5–12 cm. long, lobes 0.9–1.8 cm. long. Fruit obovoid, 2–3 cm. long, truncate at apex.

DISTRIBUTION. Endemic to eastern Cuba.

SPECIMENS EXAMINED. **Cuba.** Without further locality: *Poeppig s.n.* (MO), *Sagra s.n.* (P), *C. Wright 2678* (F, GH, K, MO, NY, P, S, YU). PINAR DEL RÍO: Sierra de Anafe, *León 2841* (GH, NY, US), *Wilson & León 11553* (NY, US); Sierra de los Organos, *Ekman 18633* (S); Sierra de San Vicente, *Ekman 18687* (S); Baños San Vicente, *Britton et al. 7420* (F, NY, US); Viñales, Sierra de la Chorrera, *León & Clemente 19050* (GH, NY, US); near Sumidero, *Shafer 13428* (NY), *13799* (NY, US); base of Sierra Guane, *Shafer 10531* (NY, US). LA HABANA: Tapaste, *Ekman 1342* (S), *León 4305* (GH, NY, US). MATANZAS: Yumury Valley, near Matanzas, *Rugel 374* (BM, GH, K, NY). SANTA CLARA: Peninsula de Zapata, near Bahía Cochinos, *Ekman 18362* (S). ORIENTE: Jauco River, *León 11731* (GH, NY, US); Moa, Río Cabanas, *Clemente & Alain 4105* (GH, NY, US); Moa, Río Cromita, *Clemente & Alain 4143* (GH, NY, US); Moa, Río Yagrumajes, *Clemente & Alain 3861* (NY); Moa, Cayoguán, *Alain & Clemente 844* (GH, NY), *Victorin et al. 21434* (US); Playa de Moa, *Acuña 12753* (US), *Clemente 4942* (GH, NY, US); Moa, *Bucher 47* (NY), *León 21239* (NY); e. of Río Moa, *Shafer 8316* (NY); Sierra de Moa, *Howard 5843* (GH); between Punta Gorda and Moa, *Thomas 511* (GH); between Moa and Cananova, *Howard 5836* (GH, NY); Yaguaneque, Cananova, *León et al. 20303* (GH, NY); Playa de la Vaca, near Moa, *Webster 3876* (GH, MICH, US); Baracoa, Río Yumurí, *León 17927* (NY); gorge of Río Yamurí, *Shafer 7854* (NY, US); Sierra de Nipe, *Ekman 6667* (F, S), *15081* (S), *15181* (S), *Howard 6174* (GH, NY), *León & Alain 19117* (GH, NY).

Cubanola daphnoides was described from a Cuban plant in cultivation at the Royal Botanic Garden, Edinburgh. Graham's description leaves no doubt that he is talking about *Cubanola* and not *Thogsennia* (also from Cuba), for he reports the plant as having a five-angled ovary and a clavate placenta. If a specimen was ever made from this plant, it has since been lost. There are no specimens of *Cubanola* at Edinburgh. Therefore, a neotype has been chosen.

Cubanola domingensis (Britton) Aiello, comb. nov.

Portlandia domingensis Britton, Bull. Torrey Bot. Club **41**: 24. 1914. TYPE: Dominican Republic. San Pedro de Macorís, San Pedro de Macorís, *Rose et al. 4176* (holotype, NY!; isotypes, GH!, NY!, US!).

Shrub or small tree up to 2 meters high. Leaves with petioles 1–3 mm. long; blades ovate or elliptic, 6–12 cm. long, 3.3–6 cm. wide, acuminate or acute at apex, obtuse or acute at base. Calyx lobes 1.1–2.5 cm. long, 1–2 mm. wide. Corolla 18.5–19.8 cm. long, tube 6.5–7 cm. long, lobes 7–8 mm. long. Fruit ellipsoid, 3–4.3 cm. long, apex obtuse.

DISTRIBUTION. Endemic to the Dominican Republic, where it is found in the provinces of Puerto Plata, Santo Domingo, San Pedro de Macorís, and La Altagracia.

SPECIMENS EXAMINED. **Dominican Republic.** PUERTO PLATA: Sosúa, *Ekman 14523* (GH, S), *Holdridge 494* (NY). SANTO DOMINGO: Caucedo, *Augusto 1360* (A, NY). SAN PEDRO DE MACORÍS: Guayacanes, *Augusto 149* (NY), *Moscoso ex Jiménez 2272* (JJ, US); San Pedro de Macorís, *Liogier 14918* (GH, IJ, NY), *Rose et al. 4176* (GH, NY, US). LA ALTAGRACIA: Playa de Macao, *Ekman 12229* (GH, K, NY, S, US); between Boca de Yuma and Cabo Falso, *Liogier 12259* (GH, NY); Saona Island, *Fairchild 2624* (A, F, US), *Marcano ex Jiménez 3390* (JJ, US).

Isidorea A. Richard ex DC. Prodr. **4**: 405. 1830. TYPE SPECIES: *Isidorea pungens* (Lam.) Robinson.

Ernodea pungens Lam. Tabl. Encycl. **1**: 276. 1791.

Shrubs or small trees of limestone areas, up to 3 meters high; all parts glabrous. Twigs grooved from base of each stipule to node below. Leaves sessile or with petioles up to 7 mm. long; blades pungent at apex, entire, coriaceous, rigid, shiny, the venation brochidodromous, with 10 to 30 pairs of closely crowded secondary and numerous higher order veins; stipules interpetiolar, narrowly triangular, aristate at apex, somewhat connate at base, eventually splitting from base to apex. Inflorescences reduced cymes in upper leaf axils; flowers 1 (to 3) in each cyme, perfect, homostylous, regular, 4- to 6-merous. Calyx lobes acicular, with colleters present on the adaxial surface. Corolla tubular or funnelform, white, red-brown, rose, pale purple, or violet, aestivation imbricate. Stamens connate for basal 1–2 mm., adnate to basal 1–2 mm. of corolla, reaching to sinuses of corolla lobes, the filaments pubescent for basal 3–6 mm., glabrous

above. Pollen tricolporate, diffusely foveolate, bearing echinate processes. Ovary 2-loculate, turbinate, the placentae linear, adnate to the septum nearly its full length, the ovules anatropous, ca. 20 per locule; style glabrous, approximately same length as stamens, the stigmatic area of 2 lines of papillae, slightly twisted around apical 3–5 mm. of style. Fruit a capsule opening loculicidally from above. Seeds perpendicular to septum, compressed and angulate due to packing, elliptic to obovate in outline, 1.5–3.2 mm. long, testa tuberculate; funicle persistent.

Eleven species endemic to Hispaniola and eastern Cuba.

The genus *Isidorea*, originally based on *Ernodea pungens* Lam., is closely allied to *Portlandia*. In both genera the fruit is a loculicidal capsule, with horizontal seeds having a tuberculate testa and a persistent funicle. *Isidorea* differs from *Portlandia* and the other genera studied: it has stiff, pungent, coriaceous leaves with numerous closely crowded secondary and higher order veins; very narrow, aristate stipules that eventually split from the base to the apex, producing an appearance of four stipules per node; twigs grooved from the base of each stipule to the node below; and, in many species, short shoots bearing leaves and flowers.

Isidorea brachycarpa (Urban) Aiello, comb. nov.

Portlandia brachycarpa Urban, Symb. Antill. **9:** 135. 1923. TYPE: Cuba, *Ekman 3758* (lectotype, S!; isotypes, F!, UPS!).

Shrub. Leaves with petioles 2–4 mm. long; blades elliptic or somewhat elliptic-obovate, 4–7 cm. long, 1–2.5 cm. wide, acute or obtuse at apex, acute at base. Flowers solitary in upper leaf axils, 5-merous. Calyx lobes 4–5 mm. long, 1 mm. wide. Corolla funnelform, 2.4 cm. long, white, the lobes 3 mm. long. Fruit obovoid-globose, 7–9 mm. long; fruiting pedicels 4–6 mm. long.

DISTRIBUTION. Known only from the type locality.

SPECIMEN EXAMINED. **Cuba.** ORIENTE: near Baracoa toward Taco Bay, *Ekman 3758* (F, S, UPS).

The holotype of this species was presumably destroyed at Berlin (B) during World War II.

Isidorea oblanceolata (Urban) Aiello, comb. nov.

Portlandia oblanceolata Urban, Symb. Antill. **9:** 136. 1923. TYPE: Cuba, *Ekman 9588* (lectotype, S!; isotypes, F!, NY!).

Shrub. Leaves with petioles 1–7 mm. long; blades oblanceolate, 2.8–9 cm. long, 0.6–1.5 cm. wide, obtuse to acute or rounded at apex, long-attenuate at base. Flowers solitary in upper leaf axils, 6-merous. Calyx lobes 0.8–1 cm. long, 1 mm. wide. Corolla unknown. Fruit obovoid, 1–1.2 cm. long; fruiting pedicels 2.8–4 cm. long.

DISTRIBUTION. Known only from the type locality.

SPECIMEN EXAMINED. **Cuba.** ORIENTE: Sierra de Nipe, in "Charrascales," along Bio path, *Ekman 9588* (F, NY, S).

The holotype of this species was presumably destroyed at Berlin (B) during World War II.

Isidorea polyneura (Urban) Aiello, comb. nov.

Portlandia polyneura Urban, Symb. Antill. **9:** 135. 1923. TYPE: Cuba. Oriente, near Miranda, El Picote, *Ekman 7403* (lectotype, S!; isotypes, F!, NY!).

Shrub. Leaves with petioles 0.3–1 cm. long; blades broadly ovate to broadly obovate or elliptic, 3.8–13 cm. long, 1.5–6 cm. wide, obtuse or acute at apex, acute to acuminate at base. Inflorescences reduced cymes in upper leaf axils; flowers 1 to 3 in each cyme, 5- (or 6-)merous. Calyx lobes 3–5 mm. long, 1 mm. wide. Corolla unknown. Fruit obovoid, 1.2–1.8 cm. long; fruiting pedicels 0.9–3 cm. long.

DISTRIBUTION. Cuba, Monte Picote, in Oriente Province.

SPECIMENS EXAMINED. **Cuba.** ORIENTE: Bayate in Monte Picote, *Ekman 7403* (F, NY, S), *9155* (F, S), *15608* (A, BM, MO, NY, S, UPS, US); near Miranda, El Picote, *López Figueiras & Morton 2426* (NY); *Morton 9710* (US), *9733* (US).

The holotype of this species was presumably destroyed at Berlin (B) during World War II.

Osa Aiello, gen. nov.

Differt a *Hintonia*: foliis longis, ad apicem attenuatis; corolla longissima, tubaeformi; seminibus magnis, tuberculatis, exalatis, non imbricatis, funiculis persistentibus.

TYPE SPECIES: *Osa pulchra* (D. Simpson) Aiello (basionym, *Hintonia pulchra* D. Simpson, 1974).

Small trees up to 15 meters high; all parts glabrous. Leaves with petioles 0.7–1.2 cm. long; blades elliptic or narrowly oblong, long-attenuate at apex and base, 16.5–19 cm. long, 4.7–5.7 cm. wide, entire, chartaceous, venation brochidodromous; stipules interpetiolar, widely triangular, acuminate to somewhat attenuate at apex, somewhat connate at base. Flowers solitary in the upper leaf axils, perfect, homostylous, regular, 5-merous. Calyx lobes subulate, 2.5 cm. long, 1 mm. wide, with colleters present on the adaxial surface. Corolla trumpet shaped, white, 26.5–27 cm. long, tube 17–18 cm. long, lobes 1.7 cm. long. Stamens connate for basal 1–3 mm., adnate to basal 1–3 mm. of corolla, reaching to sinuses of corolla lobes, filaments glabrous. Pollen tricolporate, diffusely foveolate, bearing echinate processes. Ovary 2-loculate, turbinate, placentae adnate to septum nearly its full length, the ovules anatropous, ca. 10 per locule; style glabrous, approximately same length as stamens. Fruit a capsule opening septicidal-

ly (?) from above, obovoid, 3.2 cm. long. Seeds basipetally appressed, elliptic to broadly elliptic in outline, 6.5 mm. long, testa mostly tuberculate but margins with colliculate areas; funicle persistent; embryo approximately 4.9 mm. long, in center of abundant endosperm.

One species, endemic to Osa Peninsula, Costa Rica.

Osa can be separated from *Hintonia* by several characters including the following: seeds large, plump, wingless, with tuberculate testa and persistent funicle, not imbricate in the fruit (vs. smaller, flat, winged, with reticulate testa, lacking persistent funicle, imbricate in the fruit); corolla very long, trumpet shaped (vs. funnelform); and leaves long, with attenuate apex (vs. short, with acute to acuminate apex).

Osa is more closely related to *Portlandia*, with which it shares seed characters of a tuberculate testa and a persistent funicle. It differs from this genus by having leaves that are long, narrow, and chartaceous, not broad and coriaceous; a corolla that is trumpet shaped, not funnelform or narrowly bell shaped; and fruit with seeds that are large and basipetally appressed, not small and horizontal.

The genus is named after the Osa Peninsula in Costa Rica, where the plant was discovered.

Osa pulchra (D. Simpson) Aiello, comb. nov.

Hintonia pulchra D. Simpson, Phytologia **29:** 277. 1974. TYPE: Costa Rica, *Burger & Liesner 7320* (holotype, F!; isotype, MO!).

Characters of the genus.

DISTRIBUTION. Costa Rica. Known only from the type locality.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: Osa Península, about 5 km. W. of Rincón de Osa, *Burger & Liesner 7320* (F, MO), *Burger & Stolze 5438* (F).

Thogsennia Aiello, gen. nov.

Gonianthes A. Richard in Sagra, Hist. Cuba **11:** 10. 1850 (in part), not Blume, 1823.

Differt a *Portlandia*: foliis in textura tenuibus; placentis in sectione transversa furcatis; capsula indehiscenti, ecostata; testa parum colliculosa usque reticulata.

TYPE SPECIES: *Thogsennia lindeniana* (A. Richard) Aiello (basionym, *Gonianthes lindeniana* A. Richard, 1850).

Trees of limestone areas, up to 10 meters high; all parts glabrous. Leaves with petioles 0.8–1 cm. long; blades elliptic-lanceolate or oblong-lanceolate, acute to acuminate at apex, acute at base, 12–19 cm. long, 4.5–6.5 cm. wide, entire, chartaceous to somewhat coriaceous, shiny above, venation brochidodromous; stipules interpetiolar, widely triangular, acuminate to attenuate at apex, connate at base. Flowers solitary in the upper

leaf axils, perfect, homostylous, regular, 5-merous. Calyx lobes subulate, 2.5–3.5 cm. long, 1–2 mm. wide, with colleters present on the adaxial surface. Corolla narrowly funnelform, white, aestivation imbricate, 20–26.8 cm. long, with lobes 2 cm. long. Stamens connate for basal 3 mm., adnate to basal 5 mm. of corolla, reaching to sinuses of corolla lobes, the filaments pubescent for basal 8–9.5 cm., glabrous above. Pollen tricolporate, diffusely foveolate, bearing echinate processes. Ovary 2-loculate, turbinate, the placentae twice forked in cross section, adnate to septum nearly its full length, the ovules anatropous, several hundred per locule; style glabrous, approximately same length as stamens, the stigmatic area of 2 lines of papillae, slightly twisted around apical 8 mm. of style. Fruit an indehiscent capsule, ellipsoid to oblong or somewhat obovoid, 2.2–5.4 cm. long. Seeds perpendicular to septum, compressed and angulate due to packing, broadly obovate in outline, 2.2–2.7 mm. long, testa collapsed-colliculate to reticulate, the cells long and wrinkled; embryo approximately 1.5 mm. long, in center of abundant endosperm.

One species endemic to eastern Cuba.

Thogsennia has two characters — large flowers and horizontal seeds — in common with *Portlandia* but differs greatly in its thinner leaves, its placenta that is forked in cross section, its indehiscent, unribbed capsules, and its very different seed testa pattern.

After it had been decided that plants named *Portlandia lindeniana* actually represented a distinct genus, it was discovered that they could not be maintained in the genus *Gonianthes* since that name had been used previously in the Burmanniaceae by Blume (1823). Therefore *Thogsennia*, an anagram of *Gonianthes*, was chosen for these plants. *Thogsennia* does not include *Gonianthes sagraeana* (originally *Portlandia daphnoides*, now *Cubanola daphnoides*) and therefore represents a new generic concept, not a new name for *Gonianthes*.

Thogsennia lindeniana (A. Richard) Aiello, comb. nov.

Gonianthes lindeniana A. Richard in Sagra, Hist. Cuba **11:** 10. 1850. TYPE: Cuba. Oriente, Santiago de Cuba, *Linden 1799* (holotype, P!; isotype, F!).
Portlandia gypsophila Macfadyen ex Grisebach, Fl. Brit. W. Indian Is. 324. 1861.
Portlandia lindeniana (A. Richard) Britton, Bull. Torrey Bot. Club **41:** 23. 1914.

Characters of the genus.

DISTRIBUTION. Endemic to eastern Cuba. Specimens collected at two widely distant localities in the Dominican Republic probably represent cultivated plants.

SPECIMENS EXAMINED. **Cuba.** ORIENTE: without further locality, *C. Wright 259* (BM, GH, K, MO, NY, S, YU); Cayo del Rey ad Río Jimbambay, *Ekman 4689* (S, US), *9603* (S, UPS); Bayate ad Río Jagua, *Ekman 8572* (A, F, S), *9636* (F, NY, S); Arroyo Blanca, Mayari, *Roig 159* (NY); Holguin to Myabe, *Shafer 1417* (F,

NY, US); Cedro to Paso Estancia, *Shafer 1618* (F, NY, US); Santiago de Cuba, *Linden 1799* (F, P). **Dominican Republic.** SANTO DOMINGO: Santo Domingo City, at Río Ozama, *Ekman 10905* (S, US). SANTIAGO: La Herradura, *Jiménez 4337* (JJ, US), *4414* (JJ, US).

The name *Portlandia gypsophylla* was originally "published" by Macfadyen (Fl. Jamaica 2: 216. 1837 [1850?]), where he cited in synonymy *P. acuminata* Roemer & Schultes (Syst. Veg. 5: 23. 1819). The entry is interrupted by the end of the printed material and is therefore incomplete. It is not possible to determine what plant Macfadyen had in mind, and it is evident that the description was meant to be continued. Therefore, the name must be considered as not validly published. The synonym cited, *P. acuminata*, was based on a specimen from Caracas, *Bredemeyer* (B-WILLD). This specimen (Microfiche, IDC 7440. 725: II. 2!) is a species of *Coutarea*. Later, Grisebach (1861) used the name *P. gypsophila* Macf. and supplied a complete diagnosis that agrees with the description of *Gonianthes lindeniana* A. Richard (1850), later known as *Portlandia lindeniana* (A. Richard) Britton (1914). According to S. Moore (1930), a Macfadyen specimen is not known since none exists at Kew. Why Macfadyen and Grisebach attributed this Cuban plant to Jamaica is unclear.

DISCUSSION OF REMAINING TAXA

Full descriptions are not given for the remaining taxa. Instead, their distinguishing characteristics are enumerated. None is closely related to *Portlandia*, although all at one time were included in that genus. None belongs to the Condamineeae as presently defined because they do not bear the seeds horizontally in the capsule.

Coutaportla Urban, Symb. Antill. 9: 146. 1923.

In *Coutaportla* the leaves are small, coriaceous, pale green; the stipules completely covered by colleters on the adaxial surface; the corolla white, 4-merous; the calyx lobes with red-tipped glands on the edges; the fruit flattened, both loculicidally and septicidally dehiscent, the placentae central and bearing 4 or 5 seeds, some ascending, some descending; the seeds flattened, the testa low-tuberculate with a baccate tubercle at one end of each cell.

Monotypic. Mexico.

Coutarea Aublet, Pl. Guian. 1: 314. 1775.

In *Coutarea* the leaves are chartaceous; the corolla white, sometimes tinged with pink, 5- or 6-merous, curved and gibbous at the base; the fruit flattened, loculicidally and septicidally dehiscent, the placentae linear, bearing approximately 25 vertical seeds that are flat, winged, and with reticulate testa.

The number of species in *Coutarea* is uncertain; the genus is presently in need of revision. Tropical America.

Hintonia Bullock in Hooker's Ic. Pl. 33: 1. 1935.

In *Hintonia* the leaves are chartaceous; the corolla white, 6- or 8-merous; the fruit septicidally dehiscent, the placentae large and spongy, bearing numerous basipetally imbricated seeds that are flat, winged, and with reticulate testa.

A key to the four species and one variety was given by Bullock (1935). Mexico and Guatemala.

Portlandia guatemalensis.

The generic affinities of *Portlandia guatemalensis* Standley (Jour. Wash. Acad. 18: 162. 1923) remain unknown since mature fruits and seeds have not been collected. Specimens of *P. guatemalensis* appear to be identical with those of *Coutarea lindeniana* Baillon (Adansonia 12: 300. 1879), none of which bears fruits either. If they are identical, the earlier epithet *lindeniana* has priority.

Portlandia guatemalensis differs from *Portlandia* as defined in this study in having chartaceous leaves, a racemiform-paniculate inflorescence, a spongy placenta that is central in the locule, and 6 to 8 ovules per locule.

Very young fruits (3–4 mm. long) were boiled and found to be flattened as in *Coutarea* and *Coutaportla*. Dissection revealed that the seeds are probably arranged much as in *Coutaportla*, but older fruits are needed to be sure. Young seeds (0.9 mm. long) examined under the SEM appeared to be wingless, and the testa was colliculate.

Portlandia guatemalensis may eventually be placed in *Coutaportla*, or it may represent an undescribed genus. It is not a *Portlandia*.

Guatemala and possibly Venezuela.

Schmidtottia Urban, Symb. Antill. 9: 137. 1923.

In *Schmidtottia* the leaves are coriaceous, dark above, paler beneath, bearing unicellular hairs; the corolla ochroleucous to yellow, pink, red, or purple, 5-merous; the fruit loculicidally and septicidally dehiscent, the placentae central, bearing 10 to 16 seeds, some ascending, some descending; the seeds flattened, with reticulate testa.

A key to nine of the ten species is given by Alain (Fl. Cuba 5: 30. 1962). Eastern Cuba.

Siemensia Urban, Symb. Antill. 9: 143. 1923.

In *Siemensia* the leaves are chartaceous, maculate, with raphide bundles and multicellular, uniseriate hairs; the corolla white, 5-merous; the fruit loculicidally and septicidally dehiscent, the placentae kidney shaped in cross section, central in the locule, covered with seeds except for the side opposite the septum; the seeds tiny, with deeply pitted testa and densely granulate interspaces. Based on the numerous tiny seeds, the presence of raphides, and the multicellular hairs, *Siemensia* probably belongs to the tribe Hedyotideae rather than to the Condamineeae.

Monotypic. Western Cuba.

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A REVISION OF THE GENUS TETRACTOMIA (RUTACEAE)*

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THE GENUS *Tetractomia* Hooker f. is known to occur naturally from the Malay Peninsula and Sumatra east to the Solomon Islands (see MAP 1). It is remarkably distinct from the other known genera of the Rutaceae in the Indo-Pacific area in having winged seeds in combination with 4-merous flowers, follicular fruits, and unifoliolate leaves. In this region, only *Flindersia* and *Chloroxylon* have similarly winged seeds, but these genera differ from *Tetractomia* in having 5-merous flowers, capsular fruits, and compound leaves, among other characters. The seeds of the monotypic New Guinean genus *Coombea* were originally described as being winged, but in fact they are merely sometimes compressed along part of the margin; each carpel of *Coombea* has two superposed ovules, and, when both develop into seeds, the crowding often results in a flattening of the regions in contact.

Probably the closest relative of *Tetractomia* is a Papuasian plant, *Melicope parviflora* C. T. White. Although it lacks winged seeds, this species is similar to *Tetractomia* in having a broad, flattened disc, erect carpels, and opposite, unifoliolate leaves.

Tetractomia has had a taxonomic history of error and confusion, which is surprising since it is so easy to recognize. Joseph D. Hooker established the genus in 1875 (Fl. Brit. India 1: 490, 491), basing it on three species, *T. majus* Hooker f. and *T. roxburghii* Hooker f. (*T. tetrandrum* (Roxb.) Merr.), both from Malaya, and *T. beccarii* Hooker f., from Borneo. In this original description and in a later illustration of *T. roxburghii*, Hooker (in Hooker's Ic. Pl. 16: *t. 1512*. 1886) clearly and accurately portrayed the diagnostic features of these distinctive plants. Nevertheless, in the first subsequent taxonomic treatment of the genus, Engler (Nat. Pflanzenfam. III. 4: 122. *fig. 64, Q–S*. 1896) reduced *Tetractomia* to the rank of a section of *Melicope*, apparently overlooking the winged seeds. Engler described the seeds of *Melicope* as ". . . länglich, an der abgelösten Placenta, mit krustiger, glänzender Schale," and under section TETRACTOMIA merely described them as being two per carpel.

In 1915, Ridley (Jour. Fed. Malay States Mus. 6: 141) described as new the genus *Terminthodia*, basing it on a Malayan plant, *Terminthodia viridiflora* Ridley. The holotype of this species, *Ridley 16042* (K), has opposite, unifoliolate leaves, 4-merous flowers with 4 stamens plus 4 staminodes, and winged, albuminous seeds, and is without question congeneric with the original species of *Tetractomia*. Ridley, however, incorrectly described the leaves as being alternate, apparently overlooked the sta-

* This is the eleventh in a series of papers on the Rutaceae of Malesia and Australasia.

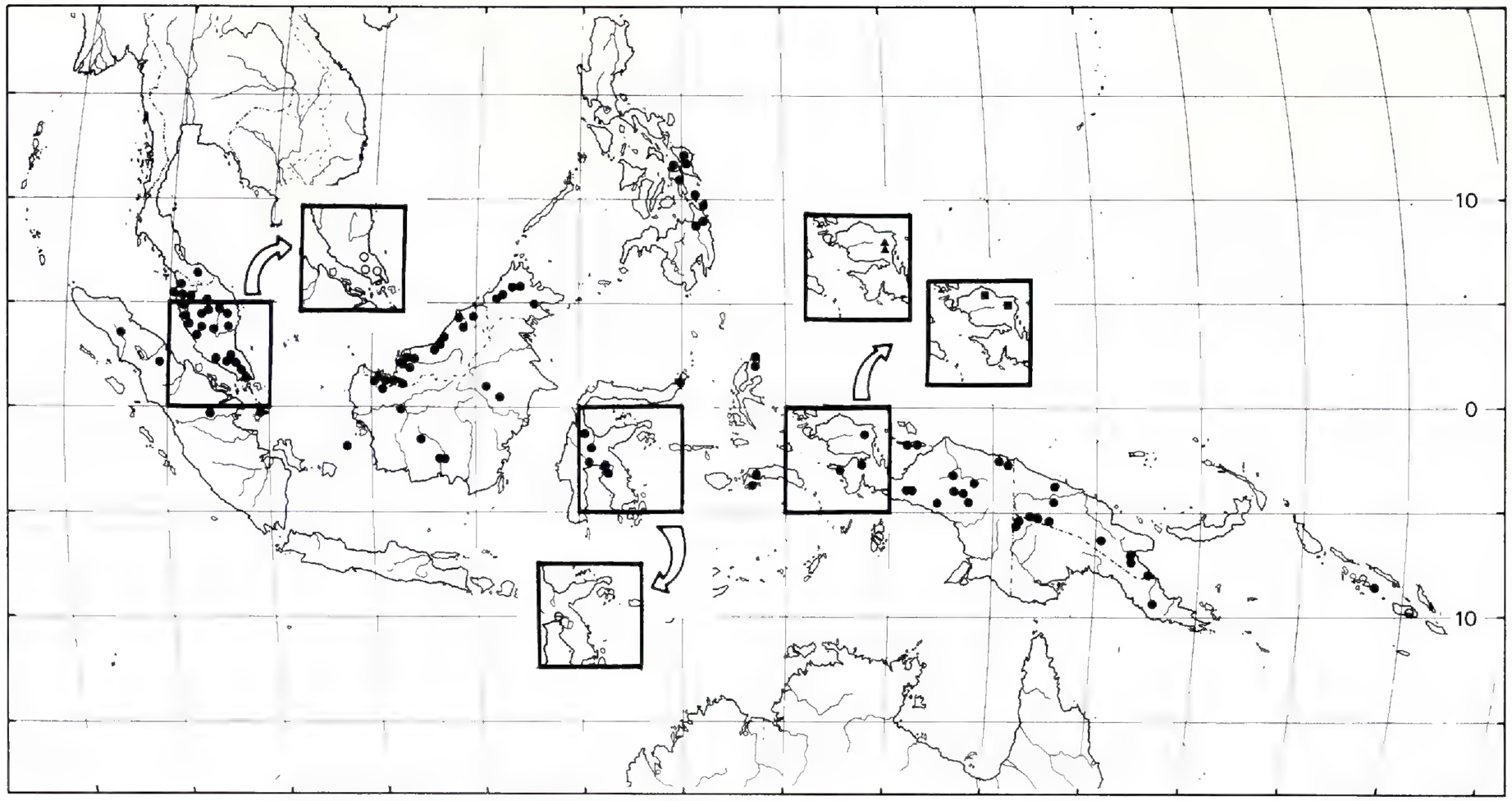
minodes, and misinterpreted the seeds as being exalbuminous. He allied the plant to *Euodia*, stating that *Terminthodia* ". . . differs in its alternate leaves, large square flat disc, and its thin-winged flat seed." The following year Ridley (Trans. Linn. Soc. London II. Bot. 9: 24. *t. 1, figs. 20–27.* 1916) described a second species of *Terminthodia*, *T. oppositifolia*, from New Guinea. Here he correctly described the leaves as being opposite, and the flowers as having 4 staminodes alternating with 4 stamens. He must have been unaware of the details of Hooker's description of *Tetractomia* because his description of this species matches it in all essential generic characters. In 1922 (Fl. Malay Penin. 1: 345, 346), Ridley recognized both *Tetractomia* and *Terminthodia* as occurring in Malaya. Again the latter was incorrectly described as having alternate leaves, only 4 stamens in the androecium, and exalbuminous seeds.

Between the years 1915 and 1930, eight additional western Malesian species were described in *Tetractomia*, six additional New Guinean species were described in *Terminthodia*, and a single New Guinean species, here excluded from *Tetractomia*, was described in *Melicope* section TETRACTOMIA. In 1931, Engler (Nat. Pflanzenfam. ed. 2. 19a: 230–233. *figs. 92, Q–S*; *97*) again treated *Tetractomia* as a section of *Melicope* and, in addition, recognized *Terminthodia* as a distinct genus. In the latter, the flowers were correctly described as having 4 stamens plus 4 staminodes, but, incorrectly, the leaves were noted to be either opposite or alternate and the seeds were described as lacking endosperm.

The first substantial clarification of this situation was made by Merrill and Perry (Jour. Arnold Arb. 22: 53–55. 1941) in their study of the Papuasian Rutaceae represented in collections of the Archbold Expeditions. They pointed out that Engler's treatment of *Tetractomia* as a section of *Melicope* seemed illogical because it placed plants with winged seeds and plants with nonwinged seeds in the same genus; this would be unusual for the Rutaceae. They also noted that all of the New Guinean species described in *Terminthodia* would be more correctly placed in *Tetractomia* and, accordingly, made the necessary new combinations.

Stone, in the only relevant publication since that of Merrill and Perry (in Whitmore, Tree Fl. Malaya 1: 385. 1972), recognized both *Tetractomia* and *Terminthodia* as occurring in Malaya. In the description of the latter, apparently based solely on *T. viridiflora*, he correctly characterized the leaves as being opposite, but incorrectly described the flowers as lacking staminodes and the seeds as being exalbuminous.

I was able to collect and study *Tetractomia* in the field while employed with the C.S.I.R.O. Phytochemical Survey of New Guinea, 1961–1965. (The results of this survey were published in Lloydia 36: 217–319. 1973.) This revision is otherwise based on herbarium specimens. The contributing herbaria, with abbreviations from Holmgren and Keuken's *Index Herbariorum*, Part 1, ed. 6 (Reg. Veg. 92. 1974), are as follows: Arnold Arboretum of Harvard University, Cambridge (A); Botanisches Museum, Berlin-Dahlem (B); Bernice P. Bishop Museum, Honolulu (BISH); Herbarium Bogoriense, Bogor (BO); Queensland Herbarium, Brisbane (BRI);



MAP 1. Distributions of *Tetractomia* species: *T. tetrandrum* (Roxb.) Merr. (dots), *T. majus* Hooker f. (circles), *T. barringtonioides* Hartley (circle with diameter line), *T. rotundifolium* (Ridley) Merr. & Perry (triangles), *T. kostermansii* Hartley (squares), and *T. solomonense* Hartley (half-filled circle).

Forest Research Institute and Colleges, Dehra Dun (DD); Botanical Survey of India, Calcutta (CAL); C.S.I.R.O. Herbarium Australiense, Canberra (CANB); Gray Herbarium of Harvard University, Cambridge (GH); Royal Botanic Gardens, Kew (K); Rijksherbarium, Leiden (L); Department of Forests, Lae, Papua New Guinea (LAE); National Herbarium of Victoria, Melbourne (MEL); National Herbarium of New South Wales, Sydney (NSW); New York Botanical Garden, New York (NY); Muséum National d'Histoire Naturelle, Paris (P); Herbarium and Library, Botanic Gardens, Singapore (SING); Botanical Museum and Herbarium, Utrecht (U); Herbarium of the University of California, Berkeley (UC); National Museum of Natural History (Department of Botany), Smithsonian Institution, Washington, D. C. (US); Naturhistorisches Museum, Wien (W); and Instytut Botaniczny, Uniwersytetu Wroclawskiego, Wroclaw, Poland (WRSL).

Tetractomia Hooker f. Fl. Brit. India 1: 490. 1875. LECTOTYPE SPECIES (chosen here): *Tetractomia majus* Hooker f.

Melicope J. R. & G. Forster section *Tetractoma* (Hooker f.) Engler in Engler & Prantl, Nat. Pflanzenfam. III. 4: 122. *fig. 64, Q–S.* 1896.

Terminthodia Ridley, Jour. Fed. Malay States Mus. 6: 141. 1915. TYPE SPECIES: *Terminthodia viridiflora* Ridley.

Shrubs or small to large trees; branchlets, buds, and leaves glabrous, or, in some specimens of *Tetractomia majus* Hooker f., leaf blades with minute, scattered, ephemeral hairs below; buds naked. Leaves opposite, unifoliolate; petiole flat adaxially, plano-convex in cross section; blade pinnately veined, entire, with scattered pellucid oil dots. Inflorescences paniculate (sometimes reduced to one or a few flowers), pedunculate, from the axils of upper leaves. Flowers bisexual, depressed-rhombic in bud; sepals 4, basally connate, valvate or basally imbricate; petals 4, distinct, valvate or slightly imbricate, acute and minutely hooked adaxially at the apex, spreading and usually becoming recurved; stamens 4, distinct, opposite the sepals, about as long as the petals at anthesis, the filament glabrous, flattened, gradually tapering from the base to a subulate apex, elongating somewhat after anthesis, the anther 2-celled, broadly ellipsoid, obtuse or obtusely mucronulate, dorsifixed, caducous; staminodes 4, alternating with the stamens, about one-half to two-thirds as long as the petals, the filament distinct or partially or entirely adherent to the petals, the anther distinct, minute, triangular, without pollen, persistent; disc intrastaminal, glabrous, broad, flattened or somewhat pulvinate, rounded to 4-angled, the angles opposite the sepals; gynoecium 4-carpellate, the carpels erect, partially embedded in the disc, joined adaxially near the apex by a single style, otherwise distinct or connate toward the base, placentation axile, the ovules 2 per carpel, collateral, the style straight, composed of 4 stylar elements twisted together, about half as long as the stamens at the time of anther dehiscence, thereafter about doubling in length, the stigma subcapitate, slightly larger in diameter than the style. Fruits of 1 to 4 erect

follicles, undeveloped carpels, if any, persistent; sepals persistent; petals, staminodes, and filaments of stamens persistent or, in *Tetractomia solomonense* Hartley, deciduous; follicles boat shaped, distinct or connate toward the base, dehiscent along the adaxial edge and down the apical abaxial edge, the outer pericarp (exocarp plus mesocarp) coriaceous, the endocarp cartilaginous, partially separating from the mesocarp. Seeds 1 or 2 per follicle, samaroid, about as long as the follicle; testa pergamentaceous, extended toward the apex of the follicle as a hyaline wing; endosperm copious, fleshy; embryo straight, elliptic, the cotyledons flattened, the hypocotyl terminal.

In his treatment of *Tetractomia* in *Flora of British India* (1: 490, 491. 1875), Hooker attributed two Malayan species to the genus, *T. majus*, which was described as new, and *T. roxburghii*, which was based on *Melicope tetrandra* Roxb. These species were numbered and listed as major entries. A third species, from Borneo, was described (also as new) in the general discussion following the description of the genus. It was referred to as "*H. beccarii.*" Also in this general discussion, and in a note following the description of *T. roxburghii*, Hooker referred to *T. majus* as "*H. majus.*" In the index to Volume 1, only *T. majus* and *T. roxburghii* are listed, but in the general index at the end of Volume 7, *T. beccarii* is listed as well, with reference to Volume 1, page 491, where "*H. beccarii*" was described.

It appears that Hooker first intended to name the genus *Hymenosperma* and then, when he decided in favor of *Tetractomia*, he (or someone else) failed to make all the necessary changes in the manuscript of his *Flora of British India*; the name *Hymenosperma* appears in Hooker's handwriting on the type sheet of *T. beccarii*, on the Roxburgh plate of *Melicope tetrandra* at Kew, and on page 43, Volume 2, of Maingay's manuscript of the *Flora of Malacca* (also at Kew), which has a description of the collection that Hooker designated as the type of *T. majus*. One of the two Kew sheets of the type collection of *T. majus* also bears the name "*H. majus*" in Hooker's handwriting.

By using the epithet *majus* for one of the original species (the other two being given genitive epithets), Hooker assigned neuter gender to the generic name *Tetractomia*. Most subsequent authors, nevertheless, have incorrectly treated the name as being feminine.

As interpreted here, *Tetractomia* consists of one widespread, polymorphic species, *T. tetrandrum*, and five local species: *T. majus*, from southern Malaya; *T. barringtonioides*, from the Celebes; *T. kostermansii* and *T. rotundifolium*, both from the Vogelkop Peninsula of New Guinea; and *T. solomonense*, from Guadalcanal. Probably the most basic differential characters of these plants are: 1) petals, staminodes, and filaments of stamens persistent vs. deciduous in fruit; and 2) leaves articulate vs. not articulate at the base of the blade. In order to arrange the species in a meaningful sequence, I am grouping them according to these characters and am assuming that the persistent flower parts and the articulated

leaf represent primitive conditions in the genus, while the deciduous flower parts and the nonarticulated leaf are derived. Thus, the species are classified as follows:

A. Petals, staminodes, and filaments of stamens persistent in fruit.
  B. Leaves articulated.
    1. *T. tetrandrum.*
    2. *T. majus.*
  B. Leaves not articulated.
    3. *T. barringtonioides.*
    4. *T. kostermansii.*
    5. *T. rotundifolium.*
A. Petals, staminodes, and filaments of stamens deciduous in fruit; leaves articulated.
    6. *T. solomonense.*

KEY TO THE SPECIES

1. Petiole 0.1–5.5 cm. long, articulated with the leaf blade, the articulation always marked in very young leaves by a transverse line of minute, caducous hairs on the adaxial side of the petiole-blade junction.
  2. Carpels in flower densely pubescent; follicles densely farinose-pubescent; petals, staminodes, and filaments of stamens deciduous in fruit. ..... 6. *T. solomonense.*
  2. Carpels in flower glabrous or occasionally sparsely pubescent; follicles glabrous or occasionally glabrate; petals, staminodes, and filaments of stamens persistent in fruit.
    3. Branchlets 2–8 mm. in diameter; leaf blades 1.1–20(–27) cm. long; pedicels 0.5–4 mm. long; petals 1–4.5 mm. long; follicles 2–11 mm. long. ..... 1. *T. tetrandrum.*
    3. Branchlets 8–13 mm. in diameter; leaf blades 11.5–26 cm. long; pedicels 5–7 mm. long; petals about 4.5 mm. long; follicles 9–11 mm. long. ..... 2. *T. majus.*
1. Petiole obsolete to 0.7 cm. long, not articulated with the leaf blade, young leaves without a transverse line of hairs at the base of the blade.
  4. Leaf blades 2–5.5 cm. long; inflorescences 0.6–3 cm. long. ..... 5. *T. rotundifolium.*
  4. Leaf blades 8–25 cm. long; inflorescences 5–22 cm. long.
    5. Inflorescences 16–22 cm. long; pedicels 0.5–1 mm. long; petals 1.3–1.5 mm. long; leaves with 8 to 11 main veins on each side of the midrib. ..... 3. *T. barringtonioides.*
    5. Inflorescences 5–7 cm. long; pedicels 1–2 mm. long; petals 2.5–3 mm. long; leaves with 6 to 8 main veins on each side of the midrib. ..... 4. *T. kostermansii.*

1. **Tetractomia tetrandrum** (Roxb.) Merr. Jour. Straits Branch Royal Asiatic Soc. 76: 87. 1917; Philip. Jour. Sci. Bot. 13: 20. 1918 (in both as "*tetrandra*").

Melicope tetrandra Roxb. Hortus Bengal. 88. 1814, *nomen nudum*; Fl. Indica, ed. 2. 2: 257. 1832; non Blanco, Fl. Filip. ed. 1. 293. 1837. LECTOTYPE (chosen here): Roxburgh Icones *1411*, Malaya, P. Penang.

Evodia pedunculosa Hooker f. Fl. Brit. India **1:** 489. 1875. TYPE: *Lobb*, Singapore.

Tetractomia beccarii Hooker f. *ibid.* **1:** 491. 1875 (as "*H. beccarii*"); *ibid.* **7:** 810. 1897 (as *T. beccarii*). TYPE: *Beccari 1880*, Sarawak.

Tetractomia roxburghii Hooker f. *ibid.* **1:** 491. 1875, *nomen illegit.*, based on *Melicope tetrandra* Roxb.

Melicope beccarii (Hooker f.) Engler in Engler & Prantl, Nat. Pflanzenfam. III. **4:** 122. 1896.

Melicope roxburghii (Hooker f.) Engler in Engler & Prantl, *ibid. fig. 64, Q–S, nomen illegit.*

Terminthodia viridiflora Ridley, Jour. Fed. Malay States Mus. **6:** 141. 1915. TYPE: *Ridley 16042*, Malaya, G. Tahan.

Tetractomia philippinense Elmer, Leafl. Philip. Bot. **8:** 2813. 1915. SYNTYPES: *Elmer 13702* & *13751*, Mindanao.

Terminthodia oppositifolia Ridley, Trans. Linn. Soc. London II. Bot. **9:** 24. *t. 1, figs. 20–27.* 1916. SYNTYPES: *Kloss* (*Wollaston Expedition*), 1913, Dutch New Guinea [Irian Jaya], Utakwa River, Camp VIb; *Kloss* (*Wollaston Expedition*), 1913, same river, Camp VIc.

Tetractomia obovata Merr. Jour. Straits Branch Royal Asiatic Soc. **76:** 86. 1917. TYPE: *Clemens 11025*, Sabah, Mt. Kinabalu.

Terminthodia obovata Lauterb. Bot. Jahrb. **55:** 246. *fig. 3.* 1918. SYNTYPES: *Gjellerup 589*, Nova Guinea Neerlandica [Irian Jaya], near Hollandia; *Schlechter 19588*, Kaiser-Wilhelmsland [Papua New Guinea], Dschischungari.

Terminthodia schultzei-leonhardi Lauterb. *ibid.* 245. TYPE: *Schultze 300*, Nordost-Neu-Guinea [Papua New Guinea], Sepik River (not seen).

Tetractomia pachyphylla Merr. Philip. Jour. Sci. Bot. **13:** 19. 1918. TYPE: *Ponce FB 26985*, Philippines, Dinagat Island.

Tetractomia acuminata Merr. *ibid.* **17:** 265. 1921. TYPE: *Ramos & Pascasio BS 35135*, Philippines, Bucas Grande Island.

Terminthodia orbiculata Markgr. Nova Guinea **14:** 143. 1924. TYPE: *Lam 1451*, Nova Guinea Neerlandica [Irian Jaya], Mt. Doorman.

Terminthodia treubiana Lauterb. Bot. Jahrb. **14:** 142. 1924. TYPE: *Pulle 1071*, Novam Guineam Meridionalem [Irian Jaya], Mt. Treub.

Tetractomia holttumi Ridley, Jour. Bot. **62:** 295. 1924. TYPE: *Holttum SF 10827*, Malaya, G. Belumut.

Terminthodia lanceolata Lauterb. Bot. Jahrb. **59:** 535. 1925. TYPE: *Ledermann 9914*, Neu-Guinea, Sepik Gebiet [Papua New Guinea, Sepik District].

Tetractomia tetrandra (Roxb.) Craib, Fl. Siam Enum. **1:** 215. 1926.

Evodia leucantha Lauterb. Bot. Jahrb. **61:** 30. 1927. TYPE: *Ledermann 11436*, New Guinea, Sepik Exped. [Papua New Guinea, Sepik District], Hunsteinspitze.

Tetractomia latifolia Ridley, Kew Bull. **1930:** 79. 1930. TYPE: *Haviland 2140*, Sarawak, Kuching.

Tetractomia montana Ridley, *ibid.* TYPE: *Haviland 2050*, Sarawak, Mt. Bongo [Bungo] near Tegora.

Tetractomia parviflora Ridley, *ibid.* 78. TYPE: *Haviland 2243*, Sarawak, near Kuching.

Melicope philippinensis (Elmer) Engler in Engler & Prantl, Nat. Pflanzenfam. ed. 2. **19a:** 233. 1931.

Tetractomia lanceolata (Lauterb.) Merr. & Perry, Jour. Arnold Arb. **22:** 54. 1941.

Tetractomia lauterbachiana Merr. & Perry, *ibid.* 55. Based on *Terminthodia obovata* Lauterb. Non *Tetractomia obovata* Merr.
Tetractomia lauterbachiana forma *pumila* Merr. & Perry, *ibid.* TYPE: *Brass 12454*, Netherlands New Guinea [Irian Jaya], Idenburg River.
Tetractomia oppositifolia (Ridley) Merr. & Perry, *ibid.* 54.
Tetractomia orbiculata (Markgr.) Merr. & Perry, *ibid.*
Tetractomia schultzei-leonhardi (Lauterb.) Merr. & Perry, *ibid.*
Tetractomia treubiana (Lauterb.) Merr. & Perry, *ibid.*

Shrub or small to large tree to about 35 meters high; branchlets 2–8 mm. in diameter. Leaves 1.2–21(–32) cm. long; petiole 0.1–4.5 cm. long, articulated with the blade; blade glabrous, chartaceous to coriaceous, suborbicular to elliptic to oblanceolate, 1.1–20(–27) cm. long, 0.9–10(–14) cm. wide, the base rounded to attenuate, the apex retuse or rounded to acuminate, the main veins 4 to 11 on each side of the midrib. Inflorescences one- to many-flowered, 0.5–19 cm. long, the peduncle, rachis, and branches glabrous to rather sparsely pubescent, the pedicels glabrous to pubescent, 0.5–4 mm. long. Flowers 2.5–10 mm. wide; sepals glabrous to sparsely pubescent, usually ciliolate when young, becoming eciliate, broadly rounded to ovate to triangular, 0.4–1.5 mm. long; petals green, white, yellow, pink, or red, entirely glabrous or rarely sparsely pubescent abaxially, ovate-triangular, 1–4.5 mm. long; stamens with anther 0.4–0.8 mm. long; carpels glabrous or occasionally sparsely pubescent, distinct at the base; style glabrous. Follicles glabrous or occasionally glabrate, distinct, 2–11 mm. long; petals, staminodes, and filaments of stamens persistent in fruit.

ILLUSTRATIONS. J. D. Hooker in Hooker's Ic. Pl. 16: *t. 1512*. 1886 (as *Tetractomia roxburghii*). Engler in Engler & Prantl, Nat. Pflanzenfam. III. 4: 122. *fig. 64, Q–S.* 1896 (as *Melicope roxburghii*). Ridley, Trans. Linn. Soc. London II. Bot. 9: 24. *t. 1, figs. 20–27*. 1916 (as *Terminthodia oppositifolia*). Lauterbach, Bot. Jahrb. 55: 246. *fig. 3*. 1918 (as *Terminthodia obovata*). Engler in Engler & Prantl, *ibid.* ed. 2. 19a: 215. *fig. 92, Q–S.* 1931 (as *Melicope roxburghii*). *Ibid.* 19a: 231. *fig. 97*. 1931 (as *Terminthodia obovata*).

DISTRIBUTION. Malay Peninsula and Sumatra east to the Solomon Islands; in various habitats (see under entities); sea level to 3300 meters (see MAP 1).

Peninsular Thailand: Pattani, Betong, G. Ina, *Kerr 7555* (K). **Malaya.** KEDAH: Jerai Reserve, *Mat Sani CF 17918* (SING). PERAK: Bubu Massif, SW. of G. Bubu, *Everett FRI 13927* (L, SING); Maxwell's Hill, *Whitmore FRI 12884* (L, SING); Taiping, *Wray 2106* (SING), *3029* (MEL); Larut, *King's Collector 5540* (W), *6194* (BO, MEL, SING, U), *6224* (BO, U), *6226* (L, US), *6994* (DD, K, L, UC), *Kunstler [King's Collector] 6194* (A); Larut Hill, *Curtis (leg. Derry) 2709* (SING); Bubu Forest Reserve, Sg. Wang, *Ng FRI 6119* (L, SING); G. Hijau, *Burkill & Haniff SF 12583* (SING); Hutan Melintang Forest Reserve, *Ng FRI 5697* (L, SING). KELANTAN: G. Stong, *Whitmore FRI 12448* (L, SING), *FRI 12459* (L, SING); G. Rabong, *Soepadmo & Mahmud 1071* (L), *1163* (BO, L). TRENGGANU: G. Padang, *Hislop*, July, 1952 (SING), *Moysey & Kiah SF 31096*

(BO, SING), *SF 31098* (SING); G. Padang Expedition, Ulu Brang, *Whitmore FRI 12648* (L, SING), *FRI 12779* (L, SING), *FRI 12793* (L, SING); G. Mandi Angin, *Cockburn FRI 10789* (L), *FRI 10810* (L), *Whitmore FRI 12061* (L), *FRI 12102* (L, SING). PAHANG: G. Tahan, *Corner*, September 12, 1937 (L), *Holttum SF 20719* (W), *Ridley 16042* (K, holotype of *Terminthodia viridiflora* Ridley), *Soepadmo 952* (L); Cameron Highlands, *Batten-Pooll*, November, 1939–January, 1940 (SING), *Carrier CF 27313* (SING), *Henderson SF 23553* (BO, NY, SING); *Ng FRI 5899* (L, SING), *Nur SF 32566* (A, L, SING); G. Tapis, *Cockburn FRI 10990* (L, SING); Fraser's Hill, *Corner*, August 10, 1937 (SING), *Ng FRI 5589* (A, L, SING), *Nur SF 11328* (BO, SING, UC). SELANGOR: Telok Forest Reserve, *Kochummen FRI 2655* (L, SING). JOHORE: Pontian, Pengkalan Raja, *Ngadiman SF 36634* (SING); G. Ledang (Mt. Ophir), *Whitmore FRI 12367* (L), *FRI 12374* (L); G. Belumut, *Holttum 65* (SING), *81* (SING), *SF 10827* (BO, isotype of *Tetractomia holttumii* Ridley); Ayer Hitam Forest Reserve, *Ng KEP 100002* (A, L, LAE, SING); Mawai-Jemulang Rd., Sg. Kayu, *Corner SF 28725* (BO, SING), *SF 28726* (BO, SING), *SF 28727* (BO, SING); Mawai, *Ngadiman SF 36797* (A, SING); G. Panti, *Chew 723* (L, SING). P. PENANG: *Curtis 281* (K, SING), *Fox*, July 23, 1905 (BO), *Henderson SF 21432* (SING), *SF 35756* (SING), Roxburgh Icones *1411* (K, lectotype of *Melicope tetrandra* Roxb.), *Kiah SF 35335* (A, BO, SING), *King's Collector 1798* (K), *4858* (W), *Kunstler* [*King's Collector*] *4858* (A), *Nauen SF 37659* (A, BO, SING), *Symington 28039* (SING). MALAYA, without definite locality: *Scortechini* (DD, K, L, MEL, SING, US, W). **Singapore:** *Lobb* (K, holotype of *Evodia pedunculosa* Hooker f.), *Maingay Kew Distribution No. 278/2* (K). **Sumatra.** RES. ATJEH (all from G. Leuser Nature Reserve): G. Ketambe & vicinity, *deWilde & deWilde-Duyfjes 13751* (L), *13997* (L), *14059* (L); G. Bandahara, *deWilde & deWilde-Duyfjes 13105* (L), *13353* (L). RIAU: Bila River, *Lörzing 14259* (L); Inderagiri, Kuala Belilas, *Buwalda 6769* (A, BRI, L, LAE). RIAU-LINGGA ARCHIPELAGO: Lingga, *Anonymous bb 5591* (BO, L). **Borneo. Sarawak.** 1ST DIVISION: Sampadi Forest Reserve, *Sinclair & Kadim 10403* (L, SING); Mt. Bongo [Bungo] near Tegora, *Haviland 2050* (K, holotype of *Tetractomia montanum* Ridley); Bungo Range, Bau, *Ilias* [*bin*] *Paie & Mamit S 29036* (L); Kuching & vicinity, *Haviland 2140* (K, holotype of *Tetractomia latifolium* Ridley), *2243* (K, holotype of *Tetractomia parviflorum* Ridley; L, isotype), *2842* (K), February 3, 1893 (P, W), February 27, 1893 (K), March 21, 1893 (BO), April 14, 1893 (BO, L), *Haviland & Hose 3358K* (K), *3359* (K), December 17, 1894 (L), *Hewitt* (BO), *Zehnder S 21598* (L, SING); Stapok, *Brunig S 17522* (L); Semengoh Forest Reserve Arboretum, *Anderson S 12578* (L, SING), *Banyeng ak Nudong & Sibat ak Luang S 26224* (L), *Galau S 15050* (L), *S 15743* (L, SING), *Haji Bujang S 32546* (L, SING), *Jugah ak Kudi* (*Tree No. 2772*) (MEL, SING), *S 14919* (L, MEL), *S 15792* (A, L), *Othman Ismawi S 32969* (L, SING), *Rosli S 14993* (L, SING), *Zen* (*Arb. No. 966*) (BO, L, SING); Mt. Penrissen, *Jacobs 5012* (CANB); Bako National Park, *Anderson 9766* (BO, L, SING), *Brunig S 7667* (L, SING), *S 7689* (L), *S 7694* (SING), *Carrick & Kassim 500* (SING), *Corner & Brunig S 10489* (L), *Ilias* [*bin*] *Paie S 17906* (A, L, SING), *Purseglove 4940* (L, NY, SING), *Shah P 5648* (L, NY, SING), *Tan SAR 28803* (SING). 2ND DIVISION: Sg. Tusak, *Anderson S 3189* (SING); 1.4 km. from Tanjong Triso, *Anderson 9792* (BO, L, SING); Lingga, *Anderson 9825* (L, SING); Saribas Forest Reserve, *Anderson 8504* (L, SING); Sg. Eutulang, *Anderson 13106* (L, SING). 3RD DIVISION: Surongirit, *Sanusi bin Tahi 5210* (BO, L, SING); Loba Kabang Protected Forest, *Anderson S 2667* (SING); Naman Forest Reserve, *Bojeng bin Sitam S 13801* (BO, L), *Hamdi S 27820* (A), *Turkey bin Tran S 27820* (L); Balingian, Ulu Sg. Arip, Bukit Iju, *Jugah ak Kudi S 23675* (A, L); Kapit, *Ilias* [*bin*]

Paie S 25828 (L, SING). 4TH DIVISION: Sg. Segan, *Brunig S 12038* (L); Penyelam, *Brunig S 8684* (L); Baram, *Anderson S 3258* (SING); Marudi Forest Reserve, *Yacup S 8264* (L, SING). SARAWAK, without definite locality: *Anderson S 2630* (SING), *Beccari 1880* (K, holotype of *Tetractomia beccarii* Hooker f.), *Brunig S 8869* (L). **Brunei:** G. Pagon Periok, *Ashton BRUN 2393* (K, L). **Kalimantan.** KALIMANTAN BARAT: G. Kelam, *Hallier 2362* (BO), *2431* (BO, L). KALIMANTAN TENGAH: Sampit District, Koealawajan, *Kostermans 8030* (CANB, SING); Sampit & vicinity, *Buwalda 7659* (BO, L), *7680* (BO, L), *7699* (BO, L), *7704* (BO, L), *7710* (BO), *7718* (BO), *7758* (BO, L), *7760* (BO, L), *7819* (BO, L), *Delmaar bb 2081* (BO), *Hackenberg 129* (B), *Kostermans 8133* (BO, L), *8155* (A, BO, L); without definite locality, *Winkler 3309* (L). KALIMANTAN TIMUR (all from West Kutei): Mt. Palimasan, on Belajan River near Tabang, *Kostermans 12721* (L), *12951A* (L), *12982* (L, SING), *13064* (L); Kowlindjan River near Melan, *Kostermans 9603* (BO, L). KARIMATA ISLAND: *Teysmann 11235* (BO). **Sabah:** Mt. Kinabalu, *Chew & Corner RSNB 4602* (K, SING), *Chew, Corner, & Stainton RSNB 265* (CANB, K, SING), *Clemens 11025* (A, isotype of *Tetractomia obovatum* Merr.), *J. & M. S. Clemens 32401* (BO, NY), *32558* (BO, L, NY, UC), *32745* (K, L, NY, UC), *33067* (L, NY, UC), *33104* (BO), *50245* (K, L, NY, UC), *50507* (K, L, NY, UC); G. Alab, *Nooteboom 969* (L); Beluran District, G. Tonsuon, *Jilimin & Kapis bin Sisiron SAN 17256* (L); Tambunan District, Crocker Range, *Chow & Aban SAN 65037* (L); *James & Aban SAN 65010* (L); Lahad Datu District, Mt. Silam, *Wood SAN A 4175* (L, SING). **Philippines.** SAMAR: Concord, *Sulit PNH 6330* (A); Mt. Calbiga, *Sulit PNH 6447* (L). BILIRAN: Mt. Suiro, *Sulit PNH 21619* (K, L), *PNH 21699* (L), *PNH 21706* (L). LEYTE: Mt. Dagami, *Ramos BS 15280* (P, US). DINAGAT: *Ponce FB 26985* (K, P, US, isotypes of *Tetractomia pachyphyllum* Merr.), *Ramos & Convocar BS 83821* (NY), *BS 83826* (NY), *BS 83906* (NY). BUCAS GRANDE: *Ramos & Pascasio BS 35106* (A, K), *BS 35135* (A, isotype of *Tetractomia acuminatum* Merr.). MINDANAO: Surigao Province, northeast coast, *Ramos & Pascasio BS 34707* (K, US); Agusan Province, Cabadbaran (Mt. Urdaneta), *Elmer 13702* (BISH, BO, CAL, GH, K, L, NSW, NY, U, US, W, isosyntypes of *Tetractomia philippinense* Elmer), *13751* (BISH, GH, K, L, NSW, NY, U, US, W, isosyntypes of *Tetractomia philippinense* Elmer). **Celebes:** Lombok, *Steup bb 15022* (BO); between Lake Lindoe and Mt. Ngilalaki, *Bloembergen 3944* (BO, L, SING); Lake Poso, *Steup bb 14901* (BO); Masamba, Kaladoe, *Anonymous bb 24168* (A, BO, L); Malili, Oesoe, *Anonymous Cel II–147*, September 12, 1934 (A, BO), *Cel II–321*, February, 1931 (L), *Cel II–321*, October 12, 1931 (BO), *Cel II–321*, October 29, 1931 (BO), *Cel II–381*, July 13, 1931 (BO), *Cel II–483*, January 20, 1931 (BO, L), *Cel III–109*, April 5, 1934 (A, BO); Malili, Waroe Waroe, *Kjellberg 2076* (BO). **Moluccas.** MOROTAI: G. Pare Pare, *Kostermans 1152* (BO, L, SING), *1207* (BO, L, LAE, SING), *1235* (L, LAE, SING); without definite locality, *Kostermans 1310* (BO, L, LAE, SING). CERAM (western): Sahoeai, *Eyma 3003* (BO, L). AMBON: Waai, Mt. Salahutu, *Eyma 3061* (BO, L), *Kuswata & Soepadmo 299* (BO, L, LAE, SING). **Papuasia. Irian Jaya:** near Fakfak, *Pleyte 1083* (BO, L); Babo, *Anonymous bb 22300* (A, BISH, L, NY, SING); Arfak Mts., Angi Lakes, *Kostermans 2454* (BO, L, SING); Wissel Lake region, *Eyma 4784* (L), *4956* (BO, L), *5229* (BO, L), *5287* (BO, L), *5368* (BO, L), *Versteegh BW 3075* (CANB); Utakwa River, Camp VIb, *Kloss (Wollaston Expedition)*, 1913 (K, isosyntype of *Terminthodia oppositifolia* Ridley); Utakwa River, Camp VIc, *Kloss (Wollaston Expedition)*, 1913 (K, isosyntype of *Terminthodia oppositifolia* Ridley); Rouffaer River, *Docters van Leeuwen 10421* (BO, L, SING); Idenburg River, vicinity of Bernhard Camp, *Brass 12016* (BO, L, LAE), *12134* (BO, L, LAE), *12172* (L, LAE), *12192* (L), *12454* (L, LAE, isotypes of *Tetractomia lauterbachianum*

forma *pumilum* Merr. & Perry), *Brass & Versteegh 11197* (BO, L, LAE); Mt. Doorman, *Lam 1451* (L, isotype of *Terminthodia orbiculata* Markgr.), *1627* (L), *1749* (L); Mt. Treub, *Pulle 1071* (BO, L, isotypes of *Terminthodia treubiana* Lauterb.); Cycloop Mts., *Koster BW 4278* (CANB, SING), *BW 4295* (BO, CANB), *van Royen & Sleumer 5838* (A, CANB, L, LAE), *6564* (A, L, LAE); Tablanoesoe, *van Royen & Sleumer 6482* (CANB); Hollandia & vicinity, *Gjellerup 589* (L, isosyntype of *Terminthodia obovata* Lauterb.), *Kostermans & Soegeng 38* (L), *445* (L), *Versteegh BW 3916* (BO, CANB, SING); Japen Island, Subdivision Seroei, *Anonymous bb 30488* (A, BO, L, SING), *Iwanggin BW 10020* (CANB, L, LAE), *BW 10073* (L, LAE), *Schram BW 10566* (L, LAE); without definite locality, *Anonymous bb 22323* (BO, L, SING). **Papua New Guinea.** SEPIK DISTRICT: Aitape Subdistrict, near Wantipi Village (on Bliri River), *Darbyshire & Hoogland 8366* (CANB); Lordberg, *Ledermann 9914* (L, isotype of *Terminthodia lanceolata* Lauterb.); Mt. Hunstein, *Ledermann 11436* (WRSL, isotype of *Euodia leucantha* Lauterb.); Telefomin Subdistrict, Oksapmin & vicinity, *Henty, Isgar, & Galore NGF 41630* (CANB, SING), *NGF 41703* (CANB); without definite locality, *Ledermann 9397* (L). WESTERN HIGHLANDS DISTRICT: Lake Kopiago, *Galore & Vandenberg NGF 41081* (CANB). EASTERN HIGHLANDS DISTRICT: near Wanatabi, about 24 km. southwest of Okapa, *Hartley 13150* (CANB). MOROBE DISTRICT: Markham Point, *Henty NGF 16757* (CANB), *Stauffer, Henty, & Whitmore 5548* (A, CANB, K, LAE); Wagau, *Womersley NGF 17824* (BO, CANB, SING); Dschischungari, *Schlechter 19588* (P, isosyntype of *Terminthodia obovata* Lauterb.). WESTERN DISTRICT: Berlin, Ok Tedi River, *Foreman & Galore NGF 45785* (CANB), *NGF 45788* (CANB); near Ingembit Village, *Henty, Ridsdale, & Galore NGF 31809* (CANB, SING). CENTRAL DISTRICT: Kokoda Trail at Ower's Corner, *Hartley 10682* (LAE). **Solomon Islands.** NEW GEORGIA GROUP: Vangunu Island, inland from Merusu Islet, *Whitmore BSIP 1213* (L, LAE, SING).

It appears to be necessary to lectotypify *Melicope tetrandra* Roxb., the basionym of this species, with the Roxburgh drawing held at Kew. I have not seen a representative Roxburgh collection, and there does not seem to be one either at Kew or at the British Museum (John Maconochie, pers. comm.).

In his description and drawing of *Melicope tetrandra*, Roxburgh did not characterize the seed as being winged, and he stated that all but the apex of the seed was enveloped in an orange-colored, fleshy aril. Perhaps the seed of fresh follicles that are very young or galled (as they sometimes are) might be interpreted in this way, or perhaps Roxburgh's material was mixed. In any case, his description and drawing otherwise clearly represent the Malayan plant interpreted here as the generalized form of *Tetractomia tetrandrum*.

Stone, in Whitmore's *Tree Flora of Malaya* (1: 385. 1972), stated that *Tetractomia tetrandrum* occurs in Burma. I have not seen any collections of it from that country.

The plants here included in *Tetractomia tetrandrum*, while very homogeneous in basic structure of vegetative and reproductive organs, are extremely variable in habit, leaf size and shape, inflorescence size, and flower and fruit size. The general pattern of this variation seems to be characterized by a widespread, generalized form of the species and several local, specialized forms (here referred to as races). This pattern seems to re-

flect the distribution of certain habitats in Malesia: the generalized form occurs mainly in tall, well-drained rain forests at lower and middle elevations, a widespread and common habitat in the region, whereas the specialized forms occur in habitats that are less common and less continuous, for example, lowland peat swamps and heath forests, and high mountain stunted forests and shrubberies.

This, however, is an over-simplification of the actual variability. Plants of the generalized form vary considerably in different parts of the range, even when growing in equivalent habitats. Also, they are not necessarily restricted in habitat preference, and intergrade locally with certain specialized forms. Intergradation also occurs *between* certain specialized forms. As a result, not one of the entities is distinct when considered in the context of all of the material of the species.

Locally distinct (or nearly distinct or otherwise noteworthy) entities do occur, however, and such workers as field botanists and foresters may find it desirable to be able to identify them. In an attempt to accommodate the needs of these people, I have prepared a geographically arranged outline of the variability within the species, with descriptions, notes on distribution, and names of relevant previously described taxa provided for the entities occurring in each region. In order to provide documentation and to facilitate identification of duplicates of the collections cited, the various entities are given letter designations (1a, 1b, etc.), which are used in the Index to Exsiccatae to refer to relevant collections. Altogether, eight entities are recognized:

The generalized form; throughout the range of the species: 1a.

Specialized forms:

1b. Malaya mountain race.
1c. Peat swamp race; Malaya, Sumatra, and Borneo.
1d. Dipterocarp forest race; Borneo.
1e. Heath forest race; Borneo.
1f. Borneo mountain race.
1g. Mossy forest race; Philippines.
1h. New Guinea mountain race.

MALAY PENINSULA

1a. The generalized form. Small to large tree. Leaves 8.5–21 cm. long; petiole 1–3.5 cm. long; blade obovate or occasionally oblanceolate or elliptic. Inflorescences many flowered, (6.5–)9–17(–19) cm. long, usually longer than the subtending leaves. Petals green to yellow to white, 1.3–2 mm. long. Follicles glabrous, 5–7.5 mm. long.

DISTRIBUTION. Southern Peninsular Thailand south to Singapore; lowland, foothill, and lower montane forests and borders; sea level to about 1500 meters; apparently restricted to well-drained sites.

Included are the types of *Tetractomia tetrandrum* (Roxb.) Merr. and *Evodia pedunculosa* Hooker f.

Intergrades with the Malaya mountain race (see below).

1b. Malaya mountain race. Shrub or small tree. Leaves 3.1–10 cm. long; petiole 0.3–1 cm. long; blade obovate to suborbicular. Inflorescences several- to many-flowered, 3.5–7 cm. long, about as long as or longer than the subtending leaves. Petals green, 1.7 mm. long. Follicles glabrous, 4.5–6 mm. long.

DISTRIBUTION. Kelantan (G. Rabong), Pahang (G. Tahan), and Johore (G. Belumut); montane forests and open places; 900–2100 meters.

Included are the type collections of *Terminthodia viridiflora* Ridley and *Tetractomia holttumii* Ridley.

A complete range of intermediates between the generalized form and the Malaya mountain race exists in Malayan forests between 900 and 1400 meters, and it is evident that the latter is merely a high mountain extreme of the former. The intermediate collections are referred to in the Index to Exsiccatae as 1a-1b.

1c. Peat swamp race. Medium tree. Leaves 8–23 cm. long; petiole 1–3.5 cm. long; blade obovate or occasionally broadly elliptic. Inflorescences few- to many-flowered, 5–11(–14.5) cm. long, shorter than the subtending leaves. Petals green, 1.3–1.5 mm. long. Follicles glabrous or glabrate, about 5 mm. long.

DISTRIBUTION. Perak, Selangor, and Johore; apparently restricted to lowland peat swamps.

The peat swamp race is reasonably distinct from the generalized form in the Malay Peninsula in having inflorescences shorter than the subtending leaves and a tendency toward smaller petals and follicles. From the data available, it also appears that here the two are ecologically distinct.

The carpels in flower and the young follicles vary from glabrous to sparsely pubescent in this entity, a character that appears to be insignificant. Such pubescence is also of sporadic occurrence in plants of the generalized form from Borneo, Celebes, and the Moluccas.

SUMATRA

1a. Generalized form. Medium tree. Leaves 12–20 cm. long; petiole 1.5–4 cm. long; blade obovate. Inflorescences several flowered, 12–17 cm. long, about as long as or longer than the subtending leaves. Petals 2 mm. long. Follicles glabrous, 7–8 mm. long.

DISTRIBUTION. Lingga; lowland peat swamp.

The collections made by deWilde and deWilde-Duyfjes from northern Sumatra (G. Leuser Nature Reserve, montane forests and open areas, 1500–2000 meters) quite closely match some of the Malayan specimens considered to be intermediate between the Malay Peninsula generalized form and the Malaya mountain race. These Sumatran collections are referred to in the Index to Exsiccatae as 1a-1b.

1c. Peat swamp race. Tree. Leaves 10.5–17 cm. long; petiole 2–2.5 cm. long; blade obovate to oblanceolate. Inflorescences several- to many-flowered, 5–7 cm. long, shorter than the subtending leaves. Petals greenish yellow, 1 mm. long. Follicles glabrate, 5–5.5 mm. long.

DISTRIBUTION. Riau; low elevation; recorded from a swampy forest.

BORNEO

1a. Generalized form. Small to large tree. Leaves 7.5–22(–32) cm. long; petiole 0.8–5 cm. long; blade obovate to oblanceolate or elliptic. Inflorescences few- to many-flowered, 4–16 cm. long, usually longer than the subtending leaves. Petals green, 1.8–2.5 mm. long. Follicles glabrous or glabrate, (3.5–)5–9 mm. long.

DISTRIBUTION. Sarawak, Kalimantan, and Sabah; lowland peat swamps and well-drained forests, borders, and open places; sea level to 1860 meters.

Included is the type collection of *Tetractomia latifolium* Ridley.

1c. Peat swamp race. Small to medium tree. Leaves 6–17 cm. long; petiole 1–3.5 cm. long; blade obovate or occasionally grading toward suborbicular or oblanceolate. Inflorescences few- to many-flowered, 2–8 cm. long, shorter than the subtending leaves. Petals green to yellowish, 1 mm. long. Follicles glabrous, about 5 mm. long.

DISTRIBUTION. Sarawak and Kalimantan; apparently restricted to lowland peat swamps.

Included is the type collection of *Tetractomia parviflorum* Ridley.

In Borneo, the peat swamp race and the generalized form are distinct in petal size, and usually in inflorescence size as well. Surprisingly, the two apparently grow together in peat swamps in the vicinities of Kuching and Sampit.

1d. Dipterocarp forest race. Medium tree. Leaves 7.5–16.5 cm. long; petiole 1–3.4 cm. long; blade obovate or occasionally oblanceolate. Inflorescences few- to several-flowered, 4.5–10.5 cm. long, shorter than the subtending leaves. Petals greenish, 3–4.5 mm. long. Follicles glabrous, 8.5–11 mm. long.

DISTRIBUTION. Sarawak; usually in lowland dipterocarp forests; one collection (*Sinclair & Kadim 10403*) from heath forest (kerangas) at low elevation.

Included is the type collection of *Tetractomia beccarii* Hooker f.

The dipterocarp forest race is very similar in leaf to several of the Borneo specimens of the generalized form, especially those from Bako National Park. The petals and follicles of the dipterocarp forest race are consistently larger, however.

Intergradation occurs between the dipterocarp forest race and the heath forest race (see text below and FIGURE 1).

1e. Heath forest race. Small tree. Leaves 2.5–5.3 cm. long; petiole 0.35–0.45 cm. long; blade obovate to oblanceolate. Inflorescences 1- to 3-flowered, 0.8–1.5 cm. long, shorter than the subtending leaves. Petals green, 3.5 mm. long. Follicles glabrous, about 7 mm. long.

DISTRIBUTION. Sarawak (Bungo Range); recorded from heath forest at about 780 meters.

Included is the type collection of *Tetractomia montanum* Ridley.

The extreme reduction in leaf and inflorescence sizes in the heath forest race is likely the result of adaptation more to edaphic conditions than to high elevation; the two collections of this race (*Haviland 2050* and *Ilias Paie & Mamit S 29036*) were probably both made from sandstone heath forests, and the maximum elevation of the Bungo Range is only 980 meters.

Four collections from heath forests and rather open, sandy areas (all from rather low elevations) in Bako National Park appear to be more or less intermediate between the dipterocarp forest and the heath forest races. These collections are referred to in the Index to Exsiccatae as 1d-1e.

The intergradation of leaf characteristics between the dipterocarp forest and the heath forest races is illustrated in FIGURE 1.

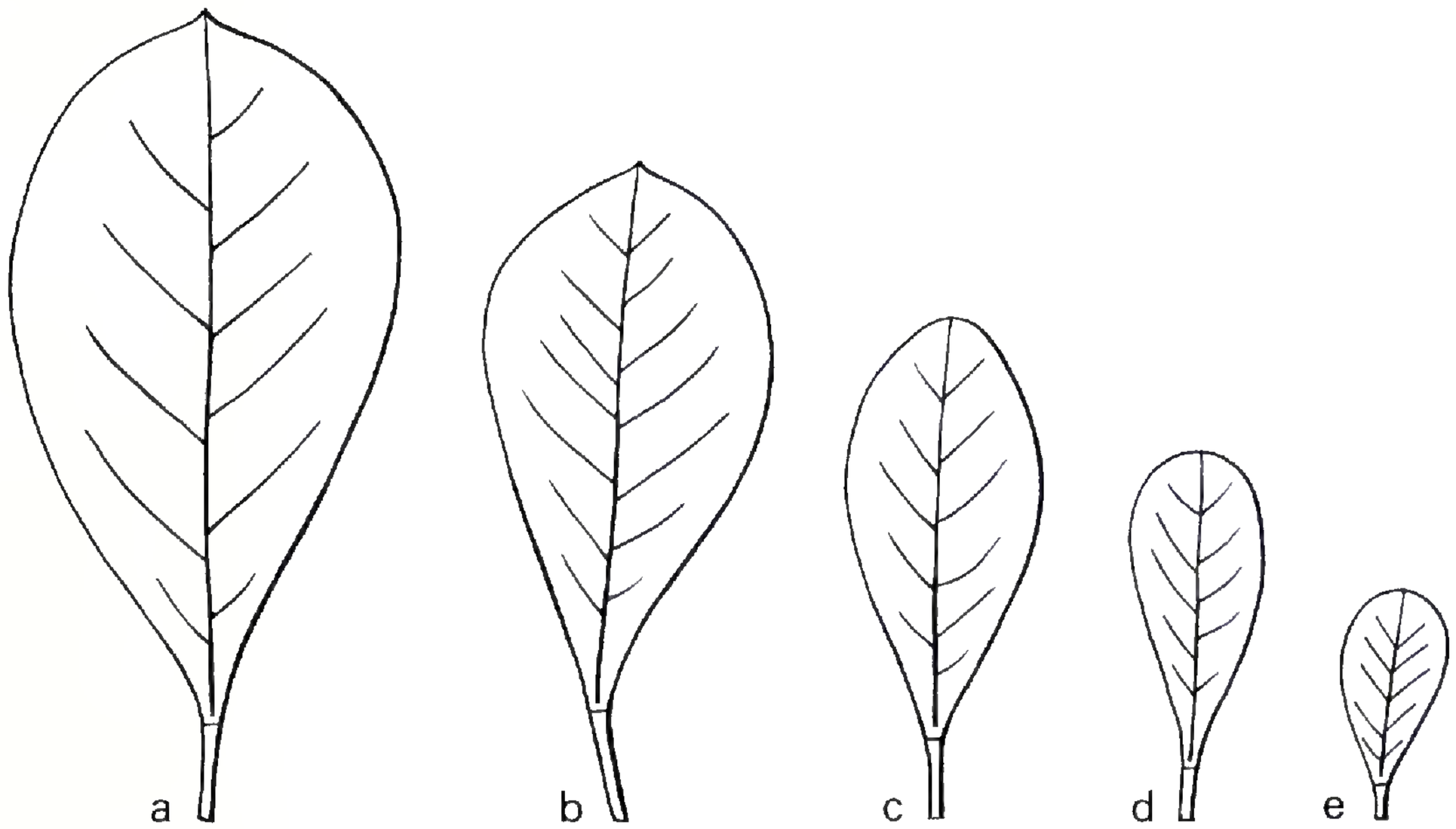


FIGURE 1. Leaf variability in *Tetractomia tetrandrum* (Roxb.) Merr. Intergradation between the dipterocarp forest race (a) and the heath forest race (e): a, *Banyeng ak Nudong & Sibat ak Luang S 26224*, from lowland dipterocarp forest, Semengoh Forest Reserve, Sarawak; b, *Jugah ak Kudi S 15792*, from dipterocarp forest at 90 meters, Semengoh Forest Reserve, Sarawak; c, *Shah P 5648*, from open sandstone summit at 210 meters, Bako National Park, Sarawak; d, *Corner & Brunig S 10489*, from open sandstone area at 150 meters, Bako National Park, Sarawak; e, *Ilias* [*bin*] *Paie & Mamit S 29036*, from sandstone heath forest at 780 meters, Bungo Range, Sarawak. (All × ½.)

1f. Borneo mountain race. Shrub or small to medium tree. Leaves 2.9–14.5 cm. long; petiole 0.3–1.5 cm. long; blade obovate to suborbicular or occasionally oblanceolate. Inflorescences few flowered, 3–8.5 cm. long, usually shorter than the subtending leaves. Petals green, greenish white, or green tinged with purple, 2.5–4 mm. long. Follicles glabrous, 5.5–7 mm. long.

DISTRIBUTION. Brunei and Sabah; lower montane forests, borders, and open places; 810–1830 meters.

Included is the type collection of *Tetractomia obovatum* Merr.

Although obviously just a lower montane extreme of the generally more lowland generalized form, the Borneo mountain race is more or less distinct from that entity in Borneo when leaf size, number of flowers per inflorescence, and petal size are considered in combination. More collections from intermediate habitats would probably show that the two intergrade completely.

Although considerably out of range, a single sterile collection from Karimata Island (*Teysmann 11235*), which has broadly obovate to suborbicular leaves, may belong to this race.

PHILIPPINES

1a. Generalized form. Shrub or small to medium tree. Leaves 8–17.5 cm. long; petiole 1–3.7 cm. long; blade obovate to oblanceolate or occasionally elliptic. Inflorescences several- to many-flowered, 9–19 cm. long, usually longer than the subtending leaves. Petals greenish yellow, 2–3.5 mm. long. Follicles glabrous, 4.5–5 mm. long.

DISTRIBUTION. Samar, Dinagat, Bucas Grande, and Mindanao; forests and borders, sea level to about 350 meters.

Included are the type collections of *Tetractomia pachyphyllum* Merr. and *T. acuminatum* Merr.

Intergrades with the mossy forest race (see below).

1g. Mossy forest race. Shrub or small tree. Leaves 4–8 cm. long; petiole 0.6–1.5 cm. long; blade obovate to oblanceolate. Inflorescences few flowered, 2–4 cm. long, shorter than the subtending leaves. Petals 1.3 mm. long. Follicles glabrous, 2.5 mm. long.

DISTRIBUTION. Mindanao (Mt. Urdaneta); mossy ridge, 1650–1725 meters.

Represented solely by the two syntype collections of *Tetractomia philippinense* Elmer.

Four Philippine collections (three from Biliran and one from Leyte; mossy forests, 900–1350 meters) appear to be more or less intermediate between the Philippine material of the generalized form and the mossy forest race. They are referred to in the Index to Exsiccatae as 1a-1g.

CELEBES

1a. Generalized form. Medium to rather large tree. Leaves 6–18 cm. long; petiole 1–3 cm. long; blade obovate to oblanceolate. Inflorescences several- to many-flowered, 5–16 cm. long, shorter than to longer than the subtending leaves. Petals 1–1.5 mm. long. Follicles glabrous or glabrate, 5–7 mm. long.

DISTRIBUTION. Minahassa Peninsula, central region, and southeastern peninsula; forests (apparently often swampy); sea level to about 2000 meters.

The Celebes plants seem more or less to combine characteristics of the Malay Peninsula-Sumatra-Borneo-Philippines material of the generalized form and the peat swamp race: in inflorescence length they tend to be more like the former, while in petal size they seem more nearly to match the latter.

MOLUCCAS

1a. Generalized form. Small to rather large tree. Leaves 6–14.5 cm. long; petiole 1.2–3.5 cm. long; blade obovate to oblanceolate. Inflorescences several flowered, 2–7 cm. long, usually shorter than the subtending leaves. Petals 1.5–2 mm. long. Follicles glabrous or rarely glabrate, 2–4 mm. long.

DISTRIBUTION. Morotai, Ceram, and Ambon; recorded from well-drained forests; sea level to about 1000 meters.

As is the case in the Celebes, the Moluccan plants of *Tetractomia tetrandrum* seem to combine characteristics of the western Malesian material of the generalized form and the peat swamp race. Here, however, the characteristics are combined in a way that is just the reverse of the way they were combined in the Celebes; in petal size the Moluccan plants resemble the generalized form, while in inflorescence size they are more like the peat swamp race.

PAPUASIA

1a. Generalized form. Small to large tree. Leaves 4.7–17.5 cm. long; petiole 0.6–3 cm. long; blade obovate to oblanceolate to elliptic or (rarely) suborbicular. Inflorescences few- to many-flowered, 2–13 cm. long, shorter than to longer than the subtending leaves. Petals white to green to pale yellow (in one collection white with pink flush), 1–2 mm. long. Follicles glabrous, 3.5–5 mm. long.

DISTRIBUTION. New Guinea and the Solomon Islands; well-drained forests (usually primary); sea level to about 1950 meters.

Included are the type collections of *Terminthodia oppositifolia* Ridley, *Terminthodia obovata* Lauterb. (*Tetractomia lauterbachianum* Merr. &

Perry), *Terminthodia orbiculata* Markgr., *Terminthodia lanceolata* Lauterb., and *Euodia leucantha* Lauterb.

Several collections, for example *Versteegh BW 3916*, *Iwanggin BW 10073*, and *Koster BW 4278*, all from Irian Jaya, and *Darbyshire & Hoogland 8366*, from the Sepik District, very closely match material of the generalized form from western Malesia; several others, including *Versteegh BW 3075* and *Eyma 5229*, both from the Wissel Lake region, and *Henty NGF 16757*, from the Morobe District, are reasonably good matches for the peat swamp race. (None of the Papuasian plants, however, seems to show a habitat preference for peat swamps.) Most of the remaining Papuasian specimens fall somewhere in between, with the result that here the differential characters of the western Malesian material of the generalized form and the peat swamp race intergrade completely. One remaining specimen, *Lam 1451*, from Mt. Doorman, an isotype of *Terminthodia orbiculata*, stands apart in having unusually large, broadly obovate to suborbicular leaf blades. In other characters, however, this specimen falls within the range of variability of the other material of the Papuasian generalized form.

The Papuasian generalized form intergrades with the New Guinea mountain race (see text below and FIGURE 2).

1h. New Guinea mountain race. Shrub. Leaves 1.2–5.5 cm. long; petiole 0.1–0.5 cm. long; blade obovate to suborbicular. Inflorescences few flowered, 0.5–2 cm. long, shorter than the subtending leaves. Petals 1.5–2 mm. long. Follicles glabrous, about 4 mm. long.

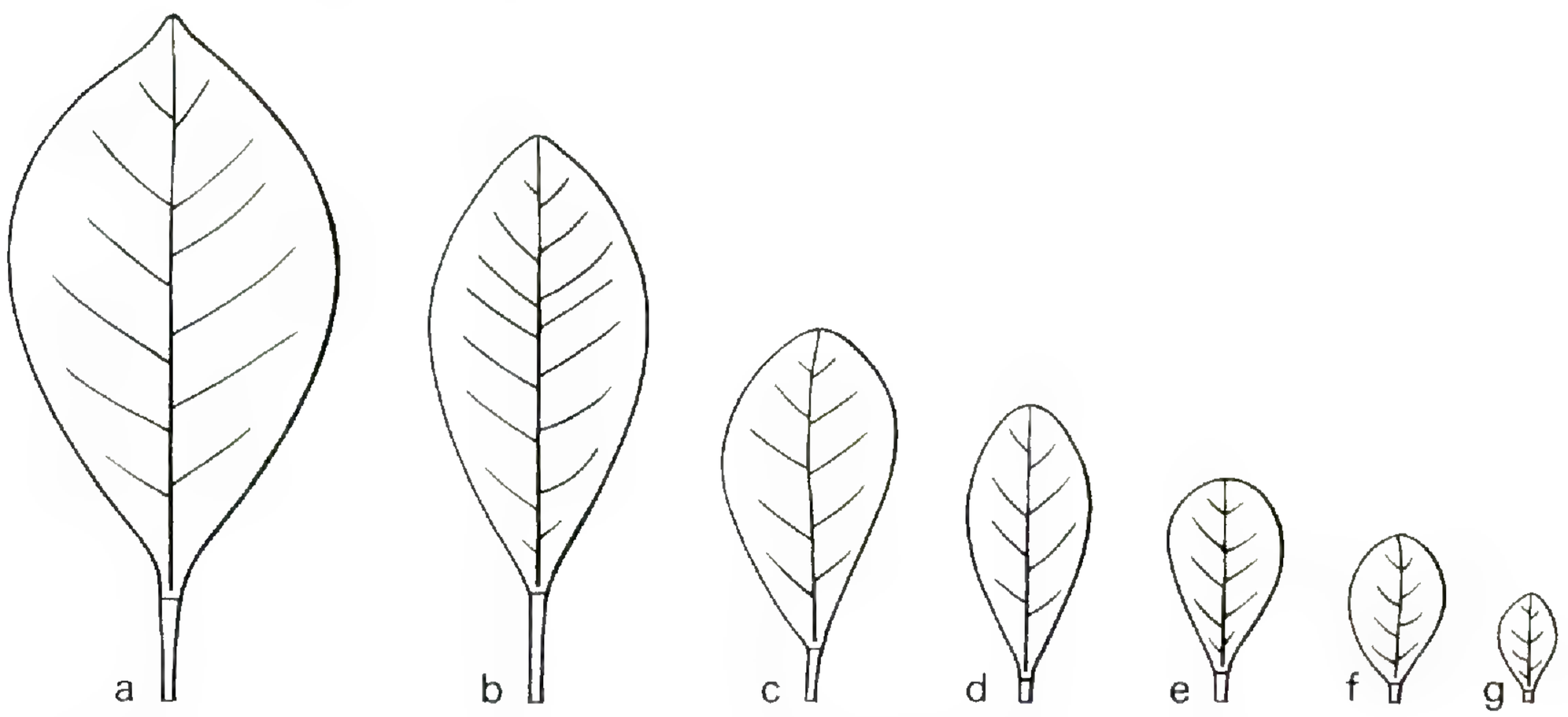


FIGURE 2. Leaf variability in *Tetractomia tetrandrum* (Roxb.) Merr. Intergradation between the New Guinea generalized form (a) and the New Guinea mountain race (g): a, *Darbyshire & Hoogland 8366*, from tall rain forest at 240 meters, Sepik District; b, *Docters van Leeuwen 10421*, from rain forest at 250 meters, Rouffaer River; c, *Brass 12134*, from mossy forest at 1800 meters, Idenburg River; d, *Kostermans 2454*, from mountain summit at 2000 meters, Arfak Mts.; e, *Brass 12192*, from mossy forest at 2100 meters, Idenburg River; f, *Lam 1627*, from subalpine shrubbery at 3300 meters, Mt. Doorman; g, *Lam 1749*, from subalpine shrubbery at 3280 meters, Mt. Doorman. (All × 0.4.)

DISTRIBUTION. Irian Jaya, Wissel Lake region and Mt. Doorman; open, subalpine habitats; about 3300 meters.

A number of specimens from Irian Jaya, including the type collections of *Terminthodia treubiana* Lauterb. and *Tetractomia lauterbachianum* forma *pumilum* Merr. & Perry, constitute a complete range of intermediates between the Papuasian generalized form and the New Guinea mountain race, and it is evident that the latter is merely a subalpine extreme of the former (see FIGURE 2). Judging from its original description, *Terminthodia schultzei-leonhardii* Lauterb. may also belong in this intermediate category. I have not seen material of the type collection (*Leonard Schultze 300*, from the Sepik District), which was apparently destroyed at Berlin in World War II.

2. **Tetractomia majus** Hooker f. Fl. Brit. India 1: 491. 1875. TYPE: *Maingay Kew Distribution No. 290*, Malaya, Malacca.

Tetramerista paniculata Kurz, London Jour. Bot. 13: 333. 1875. Based on the type collection of *Tetractomia majus* Hooker f.

Melicope major (Hooker f.) Engler in Engler & Prantl, Nat. Pflanzenfam. III. 4: 122. 1896.

Medium tree 12–15 meters high; branchlets 8–13 mm. in diameter. Leaves 13.5–30.5 cm. long; petiole 2.5–5.5 cm. long, articulated with the blade; blade glabrous or with minute, scattered, ephemeral hairs below, subcoriaceous to coriaceous, obovate to broadly oblanceolate, 11.5–26 cm. long, 6.5–12.5 cm. wide, the base cuneate to attenuate, the apex rounded or occasionally acuminate, the main veins 10 to 12 (to 16) on each side of the midrib. Inflorescences 10–16 cm. long, many flowered, the peduncle glabrate, the rachis and branches sparsely pubescent, the pedicels sparsely pubescent, 5–7 mm. long. Flowers about 9 mm. wide; sepals glabrous to sparsely pubescent, ciliolate when young, becoming eciliate, broadly ovate, about 1.5 mm. long; petals green, glabrous, ovate-triangular, about 4.5 mm. long; stamens with anther about 1 mm. long; gynoecium glabrous, the carpels distinct at the base. Follicles glabrous, distinct, 9–11 mm. long; petals, staminodes, and filaments of stamens persistent in fruit.

DISTRIBUTION. Southern Malaya; lowland peat swamps (see MAP 1).

Malaya. MALACCA: *Maingay Kew Distribution No. 290* (K, holotype of *Tetractomia majus* Hooker f.; L, isotype). JOHORE: Pontian, Pengkalan Raja, *Ngadiman SF 36674* (A), *SF 36684* (SING); Ayer Hitam Forest Reserve, *Kochummen FRI 2148* (L, SING); Sedili Botanic Reserve, *Corner SF 35561* (L, SING).

Tetractomia majus was published in February, 1875; *Tetramerista paniculata*, in November, 1875.

Tetractomia majus is very closely related to *T. tetrandrum*, differing mainly in having thicker branchlets and longer pedicels. The two species (the latter as the peat swamp race) appear to grow together in two localities in Johore.

FIGURE 3. *Tetractomia barringtonioides* Hartley: a, fertile branchlet, × ½; b, flower with one petal removed, × 11; c, fruit in abaxial view, × 5; d, fruit with adaxial view of single follicle containing seed, × 5; e, seed, × 5. (Drawn from *Anonymous CEL II–361*, June 12 to July 13, 1931.)

3. **Tetractomia barringtonioides** Hartley, sp. nov. FIGURE 3.

Arbor mediocris vel magna usque 30 m. alta; ramulis 5–10 mm. latis; foliis 10–25 cm. longis; petiolo obsoleto vel usque 0.7 cm. longo, basi laminae non articulato; lamina glabra, subcoriacea, oblanceolata, 10–25 cm. longa, 4.5–12.5 cm. lata, basi attenuata, apice rotundata vel obtusa, venis primariis utrinsecus costae 8–11; inflorescentiis multifloris, 16–22 cm. longis, pedunculo glabro vel glabrato, rhachidi et ramis sparse vel aliquantum dense pubescentibus, pedicellis sparse vel aliquantum dense pubescentibus, 0.5–1 mm. longis; floribus 2.5–3 mm. latis; sepalis glabris, ovato-triangularibus, 0.5–0.7 mm. longis; petalis albis vel pallide viridibus, glabris, ovato-triangularibus, 1.3–1.5 mm. longis; staminibus anthera ca. 0.5 mm. longa; gynoecio glabro, carpellis basi distinctis; folliculis glabris, distinctis, 5–5.5 mm. longis; petalis, staminodiis, et filamentis staminum in fructu persistentibus. HOLOTYPUS: *Anonymous Cel II–361*, May 28, 1931 (L).

DISTRIBUTION. Celebes, Malili; primary forests; sea level to 200 meters (see MAP 1).

Celebes: Malili, Oesoe, *Anonymous Cel II–361*, May 28, 1931 (L, holotype; BO, K, isotypes), *Cel II–361*, June 12, 1931 (BO), *Cel II–361*, June 12–July 13, 1931 (K, L), *Cel III–30*, October 27, 1931 (BO, L), *Cel III–30*, December 8, 1931 (BO, L), *Cel III–30*, July 8, 1932 (L).

As is noted above, *Tetractomia barringtonioides*, *T. kostermansii*, and *T. rotundifolium* appear to comprise a natural group differing from the other species of the genus in not having an articulation at the base of the leaf blade. Within the group, the three species differ quite significantly (although only quantitatively), and their interrelationships are not particularly clear.

The epithet *barringtonioides* refers to the similarity of the leaves of this species to those of some of the species of *Barringtonia* (Lecythidaceae) (*B. asiatica* (L.) Kurz and *B. calyptrata* (Miers) R. Br. ex F. M. Bailey, for example).

4. **Tetractomia kostermansii** Hartley, sp. nov. FIGURE 4.

Arbor parva 3–5 m. alta; ramulis 4–5 mm. latis; foliis 8–17 cm. longis; petiolo obsoleto vel usque 0.5 cm. longo, basi laminae non articulato; lamina glabra, coriacea, obovata vel oblanceolata, 8–17 cm. longa, 4–7 cm. lata, basi attenuata, apice retusa vel rotundata vel obtusa, venis primariis utrinsecus costae 6–8; inflorescentiis pluri- vel multifloris, 5–7 cm. longis, glabris, pedicellis 1–2 mm. longis; floribus ca. 6 mm. latis; sepalis glabris, late rotundatis vel ovato-triangularibus, 0.8–1 mm. longis; petalis glabris, ovato-triangularibus, 2.5–3 mm. longis; staminibus anthera ca. 0.6 mm. longa; gynoecio glabro, carpellis basi distinctis vel basin versus connatis; folliculis glabris, distinctis vel basin versus connatis, 4–5.5 mm. longis; petalis, staminodiis, et filamentis staminum in fructu persistentibus. HOLOTYPUS: *Kostermans 2192* (L).

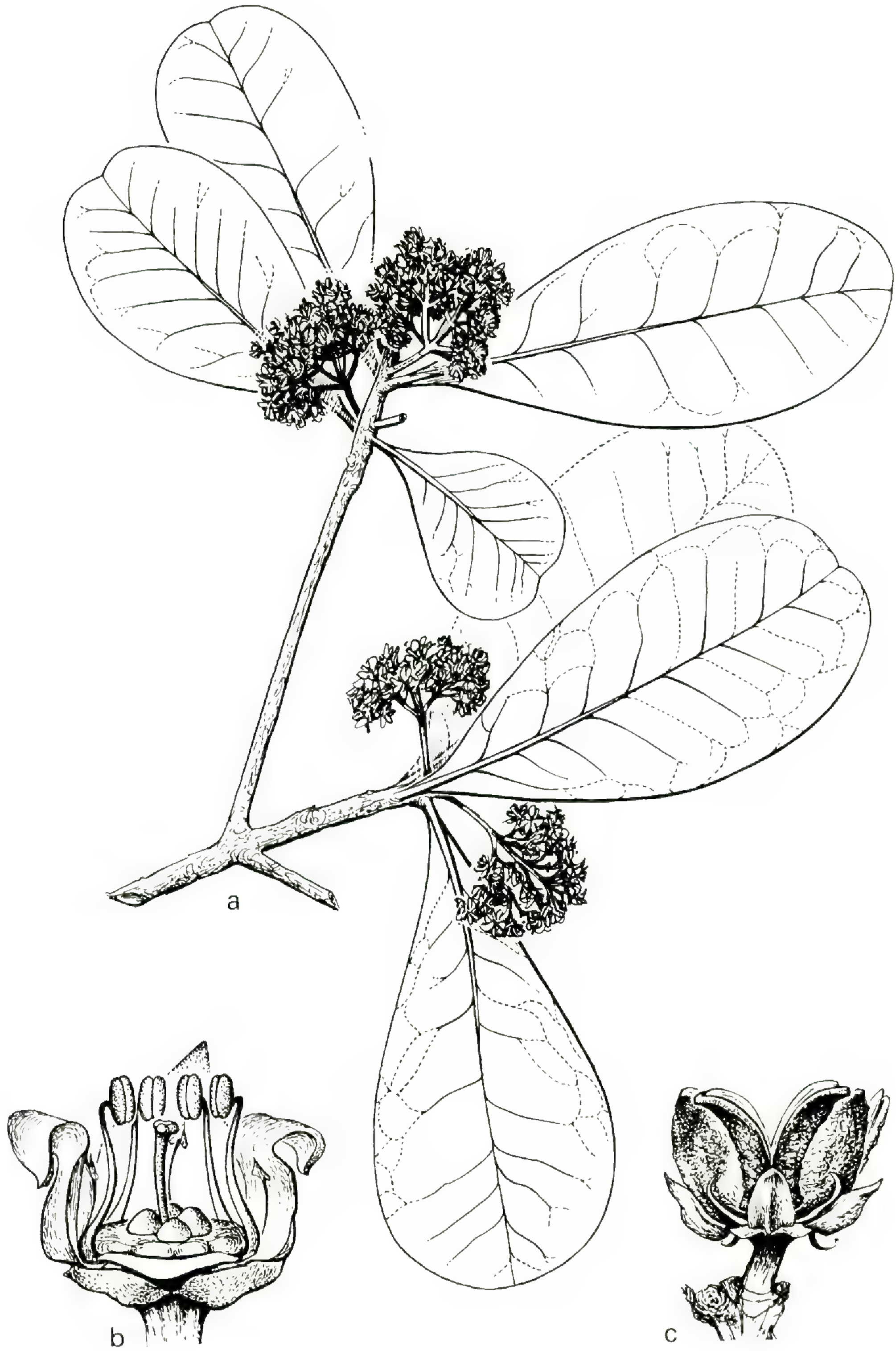


FIGURE 4. *Tetractomia kostermansii* Hartley: a, fertile branchlet, × 0.45; b, flower with one petal removed, × 10; c, fruit, × 4.5. (Drawn from *Kostermans 2418*.)

DISTRIBUTION. Irian Jaya, Vogelkop Peninsula; montane forests; 1800–1850 meters (see MAP 1).

Papuasia. IRIAN JAYA. Vogelkop Peninsula: Nettoti Range, N. slope of Mt. Nettoti, *van Royen & Sleumer 8167* (L); Arfak Mts., Angi Lakes, *Kostermans 2192* (L, holotype; BO, SING, isotypes), *2418* (BO, L, SING).

It is noteworthy that *Tetractomia kostermansii*, *T. rotundifolium*, and *T. tetrandrum* have all been collected in the vicinity of the Angi Lakes. Whether or not all three grow side by side at this locality cannot be determined from the data available, but this seems possible. The collections of *T. kostermansii* were made from forests at 1800 meters, while those of *T. rotundifolium* were made from both forests and open areas from 1900 to 2700 meters. The single collection of *T. tetrandrum* (*Kostermans 2454*, an intermediate between the generalized form and the New Guinea mountain race) was recorded from a mountain summit at 2000 meters (probably an open habitat: Kostermans made other collections of *Tetractomia* on this trip to the Angi Lakes and clearly indicated when the plants were growing in forested habitats), but plants similar to those of Kostermans also grow in montane forests elsewhere in Irian Jaya.

5. Tetractomia rotundifolium (Ridley) Merr. & Perry, Jour. Arnold Arb. 22: 54. 1941 (as "*rotundifolia*").

Terminthodia rotundifolia Ridley in Gibbs, Contr. Phytogr. Fl. Arfak Mts. 143. 1917. TYPE: *Gibbs 5653*, Dutch N.W. New Guinea [Irian Jaya], Arfak Mts.

Small to rather tall shrub to about 4 meters high; branchlets 2–3 mm. in diameter. Leaves 2–5.5 cm. long; petiole obsolete to 0.15 cm. long, not articulated with the blade; blade subcoriaceous to coriaceous, suborbicular to obovate to oblanceolate, 2–5.5 cm. long, 1–2.5 cm. wide, the base cuneate to attenuate, the apex rounded to obtuse, the main veins 4 or 5 on each side of the midrib. Inflorescences one- to few-flowered, 0.6–3 cm. long, glabrous or nearly so, the pedicels 1–2 mm. long. Flowers about 5 mm. wide; sepals glabrous, eciliate, triangular, about 1 mm. long; petals glabrous, ovate-triangular, about 2 mm. long; stamens with anther 0.5 mm. long; gynoecium glabrous, the carpels distinct at the base. Follicles glabrous, distinct, about 4 mm. long; petals, staminodes, and filaments of stamens persistent in fruit.

DISTRIBUTION. Irian Jaya, Arfak Mts.; montane forests and open places; 1900–2700 meters (see MAP 1).

Papuasia. IRIAN JAYA. Arfak Mts.: Angi Lakes, *Kanehira & Hatusima 13491* (A, BO), *Kostermans 2462* (BO, L); Angi Lakes, Mt. Koebré, *Gibbs 5653* (K, isotype of *Terminthodia rotundifolia* Ridley), *Kanehira & Hatusima 13703* (A), *14082* (A).

Ridley listed the type of this species as *Gibbs 5652*. This is apparently an error. The type sheet at Kew bears the number *5653*. Also, *Gibbs*

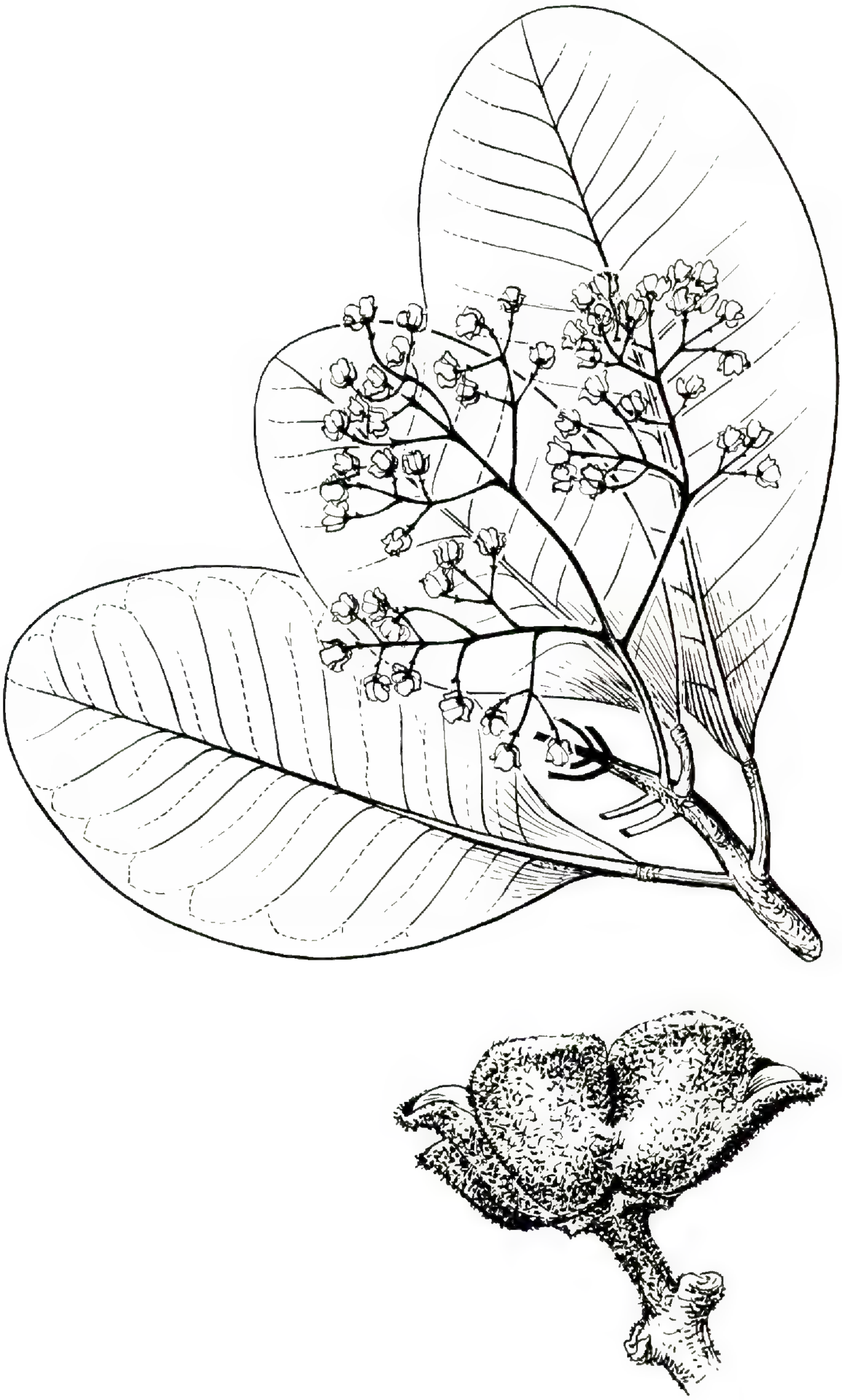


FIGURE 5. *Tetractomia solomonense* Hartley: above, fertile branchlet, × 0.7; below, fruit, × 7. (Drawn from *Gafui & Collectors BSIP 9465*.)

5652 is cited as a syntype of *Microstylis grandiflora* J. J. Sm. in Gibbs's *Contribution to the Phytogeography and Flora of the Arfak Mts.* 111. 1917.

6. Tetractomia solomonense Hartley, sp. nov. FIGURE 5.

Arbor mediocris ca. 12 m. alta; ramulis 5–6 mm. latis; foliis 10–14.5 cm. longis; petiolo 1–1.5 cm. longo, basi laminae articulato; lamina glabra, subcoriacea, subelliptica vel obovata, 9–13 cm. longa, 4.5–7 cm. lata, basi cuneata, apice rotundata, venis primariis utrinsecus costae 9–10; paniculis fructiferis 7–16 cm. longis, pedunculo glabrato, rhachidi et ramis sparse pubescentibus, pedicellis aliquantum dense pubescentibus, 1–4 mm. longis; floribus (descriptio ex parte ex partibus delapsis florum) ca. 3.5 mm. latis; sepalis pubescentibus, triangularibus vel ovato-triangularibus, 0.5 mm. longis; petalis glabris, ovato-triangularibus, 1.5 mm. longis; staminibus anthera ca. 0.5 mm. longa; carpellis dense pubescentibus, basin versus connatis; stylo glabro; folliculis dense farinoso-pubescentibus, basin versus connatis, ca. 3.5 mm. longis; petalis, staminodiis, et filamentis staminum in fructu deciduis. HOLOTYPUS: *Gafui & Collectors BSIP 9465* (K).

DISTRIBUTION. Known only from the type collection (see MAP 1).

Papuasia. SOLOMON ISLANDS. Eastern Guadalcanal: Makini area, Marau, *Gafui & Collectors BSIP 9465* (K, holotype; L, LAE, isotypes).

EXCLUDED SPECIES

Melicope (section Tetractomia) *lamii* Lauterb. Nova Guinea **14:** 142. 1924 (as section "Tetractoma"). The two syntypes of this species, *Lam 1841* and *1863*, both from Mt. Doorman, Irian Jaya ("Nova Guinea Neerlandica" on labels), have trifoliolate, or predominantly trifoliolate, leaves and functionally pistillate flowers, each with 8 staminodes. They clearly do not belong in *Tetractomia*, but are probably correctly placed in *Melicope*.

ACKNOWLEDGMENTS

I wish to thank the directors and curators of the herbaria listed in the introduction for making specimens in their care available to me. Thanks are also extended to Tibor Binder, C.S.I.R.O. Division of Plant Industry, who prepared the illustrations, and to John Maconochie, the Australian Botanical Liaison Officer at Kew in 1977, who very helpfully supplied me with information regarding Roxburgh's drawing of *Melicope tetrandra* and Maingay's *Flora of Malacca* manuscript.

INDEX TO EXSICCATAE

The numbers in parentheses refer to the corresponding species in the text. The entities of species number 1, *Tetractomia tetrandrum*, are referred to by letters, following the outline given in the text.

Anderson *S 2667* (1a); *S 2630* (1c); *S 3189* (1a); *S 3258* (1c); *8504*, *9766* (1a); *9792*, *9825* (1c); *S 12578* (1d); *13106* (1c).

Ashton *BRUN 2393* (1f).

Banyeng ak Nudong & Sibat ak Luang *S 26224* (1d).

Beccari *1880* (1d).

Bloembergen *3944* (1a).

Bojeng bin Sitam *S 13801* (1a).

Bosschen buitengewesten series (*bb*), Netherlands Indies Forest Service; the following by anonymous collectors: *bb 5591*, *bb 22300*, *bb 22323*, *bb 24168*, *bb 30488* (1a).

Brass *12016*, *12134*, *12172*, *12192*, *12454* (1a-1h).

Brass & Versteegh *11197* (1a-1h).

Brunig *S 7667*, *S 7689* (1a); *S 7694* (1d); *S 8684*, *S 8869* (1a); *S 12038* (1c); *S 17522* (1a).

Burkill & Haniff *SF 12583* (1a-1b).

Buwalda *6769*, *7659*, *7680*, *7699* (1c); *7704*, *7710* (1a); *7718*, *7758* (1c); *7760* (1a); *7819* (1c).

Carrick & Kassim *500* (1a).

Carrier *CF 27313* (1a-1b).

Celebes series, Forest Research Institute, Buitenzorg; the following by anonymous collectors: *Cel II–147*, *Cel II–321* (1a); *Cel II–361* (3); *Cel II–381*, *Cel II–483* (1a); *Cel III–30* (3); *Cel III–109* (1a).

Chew *723* (1a).

Chew & Corner *RSNB 4602* (1f).

Chew, Corner, & Stainton *RSNB 265* (1a).

Chow & Aban *SAN 65037* (1a).

Clemens, J. & M. S. *32401*, *32558*, *32745*, *33067*, *33104* (1f); *50245* (1a); *50507* (1f).

Clemens, M. S. *11025* (1f).

Cockburn *FRI 10789*, *FRI 10810*, *FRI 10990* (1a).

Corner *SF 28725*, *SF 28726*, *SF 28727* (1c); *SF 35561* (2).

Corner & Brunig *S 10489* (1d-1e).

Curtis *281* (leg. Derry) *2709* (1a).

Darbyshire & Hoogland *8366* (1a).

Delmaar *bb 2081* (1a).

Docters van Leeuwen *10421* (1a).

Elmer *13702*, *13751* (1g).

Everett *FRI 13927* (1a).

Eyma *3003*, *3061* (1a); *4784* (1h); *4956* (1a-1h); *5229* (1a); *5287*, *5368* (1a-1h).

Foreman & Galore *NGF 45785*, *NGF 45788* (1a).

Gafui & Collectors *BSIP 9465* (6).

Galau *S 15050*, *S 15743* (1d).

Galore & Vandenberg *NGF 41081* (1a).

Gibbs *5653* (5).

Gjellerup *589* (1a).

Hackenberg *129* (1c).

Haja Bujang *S 32546* (1d).

Hallier *2362*, *2431* (1a).

Hamdi *S 27820* (1a).

Hartley *10682*, *13150* (1a).

Haviland *2050* (1e); *2140* (1a); *2243* (1c); *2842* (1a).

Haviland & Hose *3358K*, *3359* (1a).

Henderson *SF 21432*, *SF 23553*, *SF 35756* (1a).

Henty *NGF 16757* (1a).

Henty, Isgar, & Galore *NGF 41630*, *NGF 41703* (1a).

Henty, Ridsdale, & Galore *NGF 31809* (1a).

Holttum *65*, *81* (1a-1b); *SF 10827*, *SF 20719* (1b).

Ilias [bin] Paie *S 17906* (1d-1e); *S 25828* (1a).

Ilias [bin] Paie & Mamit *S 29036* (1e).

Iwanggin *BW 10020*, *BW 10073* (1a).

Jacobs *5012* (1a).

James & Aban *SAN 65010* (1a).

Jilimin & Kapin bin Sisiron *SAN 17256* (1f).
Jugah ak Kudi *Tree No. 2772*, *S 14919*, *S 15792* (1d); *S 23675* (1a).
Kanehira & Hatusima *13491*, *13703*, *14082* (5).
Kerr *7555* (1a).
Kiah *SF 35335* (1a).
King's Collector *1798*, *4858*, *5540*, *6194*, *6224*, *6226*, *6994* (1a).
Kjellberg *2076* (1a).
Kochummen *FRI 2148* (2); *FRI 2655* (1c).
Koster *BW 4278*, *BW 4295* (1a).
Kostermans *1152*, *1207*, *1235*, *1310* (1a); *2192*, *2418* (4); *2454* (1a-1h); *2462* (5); *8030* (1a); *8133*, *8155* (1c); *9603*, *12721*, *12951A*, *12982*, *13064* (1a).
Kostermans & Soegeng *38*, *445* (1a).
Kunstler *4858*, *6194* (1a).
Kuswata & Soepadmo *299* (1a).
Lam *1451* (1a); *1627*, *1749* (1h).
Ledermann *9397*, *9914*, *11436* (1a).
Lörzing *14259* (1c).
Maingay *Kew Distribution No. 278/2* (1a); *Kew Distribution No. 290* (2).
Mat Sani *17918* (1a-1b).
Moysey & Kiah *SF 31096*, *SF 31098* (1a-1b).
Nauen *SF 37659* (1a).
Ng *FRI 5589* (1a); *FRI 5697* (1c); *FRI 5899*, *FRI 6119* (1a); *KEP 100002* (1c).
Ngadiman *SF 36634* (1c); *SF 36674*, *SF 36684* (2); *SF 36797* (1c).
Nooteboom *969* (1a).
Nur *SF 11328* (1a-1b); *SF 32566* (1a).
Othman Ismawi *S 32969* (1d).
Pleyte *1083* (1a).
Ponce *FB 26985* (1a).
Pulle *1071* (1a-1h).
Purseglove *4940* (1a).
Ramos *BS 15280* (1a-1g).
Ramos & Convocar *BS 83821*, *BS 83826*, *BS 83906* (1a).
Ramos & Pascasio *BS 34707*, *BS 35106*, *BS 35135* (1a).
Ridley *16042* (1b).
Rosli *S 14993* (1d).
van Royen & Sleumer *5838*, *6482*, *6564* (1a); *8167* (4).
Sanusi bin Tahi *5210* (1c).
Schlechter *19588* (1a).
Schram *BW 10566* (1a).
Shah *P 5648* (1d-1g).
Sinclair & Kadim *10403* (1d).
Soepadmo *952* (1b).
Soepadmo & Mahmud *1071*, *1163* (1b).
Stauffer, Henty, & Whitmore *5548* (1a).
Steup *bb 14901*, *bb 15022* (1a).
Sulit *PNH 6330*, *PNH 6447* (1a); *PNH 21619*, *PNH 21699*, *PNH 21706* (1a-1g).
Symington *28039* (1a).
Tan *SAR 28803* (1d-1e).
Teysmann *11235* (1f).
Turkey bin Tran *S 27820* (1a).
Versteegh *BW 3075*, *BW 3916* (1a).
Whitmore *BSIP 1213*, *FRI 12061* (1a); *FRI 12102*, *FRI 12367*, *FRI 12374* (1a-1b); *FRI 12448* (1a); *FRI 12459*, *FRI 12648* (1a-1b); *FRI 12779*, *FRI 12793*, *FRI 12884* (1a).
deWilde & deWilde-Duyfjes *13105*, *13353*, *13751*, *13997*, *14059* (1a-1b).
Winkler *3309* (1a).
Womersley *NGF 17824* (1a).
Wood *SAN A 4175* (1f).
Wray *2106*, *3029* (1a).
Yacup *S 8264* (1a).
Zehnder *S 21598* (1c).
Zen *Arboretum No. 966* (1d).

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NEW SPECIES AND VARIETIES FROM THE BAHAMAS, CAICOS AND TURKS ISLANDS

DONOVAN S. CORRELL

AS NOTED IN an earlier paper (Jour. Arnold Arb. 58: 40–51. 1977), my extensive field explorations in the Bahamas, Caicos and Turks Islands continue to yield new entities. The following are the latest of these. Holotypes have been placed in the Herbarium of the Arnold Arboretum, Harvard University; isotypes are in the Fairchild Tropical Garden Herbarium and elsewhere as indicated.

GRAMINEAE

Dichanthelium caerulescens (Hack. ex Hitchc.) Correll, comb. nov.

Panicum caerulescens Hack. ex Hitchc. Contr. U. S. Natl. Herb. 12: 219. 1909.

Gould, in Brittonia 26: 59. 1974, elevated the subgenus DICHANTHELIUM Hitchc. & Chase in *Panicum* L. to the status of genus. In following Gould, with whom I agree, it is necessary to make the present combination for my forthcoming *Flora*.

PORTULACACEAE

Portulaca minuta Correll, sp. nov. FIGURE 1.

Perennis. Caudex incrassatus plerumque fusiformis usque 2 cm. longus et 5 mm. crassus. Caules plures e basi, erecto-patentes, succulenti, raro plus quam 3 cm. longi. Folia opposita, obovata vel obovato-elliptica, plana sed carnoso-crassa. Flores solitarii ad apicem caulium et ramorum. Sepala 2, suborbicularia, concava. Petala 4, aurea, obovato-cuneata, emarginata, circa 3 mm. longa. Stamina 8, longitudine irregularia. Stylus trilobus. Fructus circa 3 mm. longus et 2 mm. latus.

TYPE. Bahamas. Great Exuma, in shallow soil of depressions in thinly coppice-covered rock flats, Hooper's Bay area west of George Town; plants succulent, leaves obovate, flowers golden yellow, July 8, 1978, *D. S. Correll 49976* (A, holotype; F, FTG, MO, NY, US, isotypes).

Plant perennial from a thickened, usually fusiform rootstock to about 2 cm. long and 5 mm. thick; stems several from the base, erect-spreading, succulent, rarely more than 3 cm. long. Leaves opposite; petiole to about 1 mm. long; blade obovate to obovate-elliptic, flat but fleshy-thickened, to about 5 mm. long and 3 mm. wide above the middle, minutely glandular, usually with a few short bristles in the axils. Flowers solitary at apex of stems and branches. Sepals 2, suborbicular, concave, about half as long

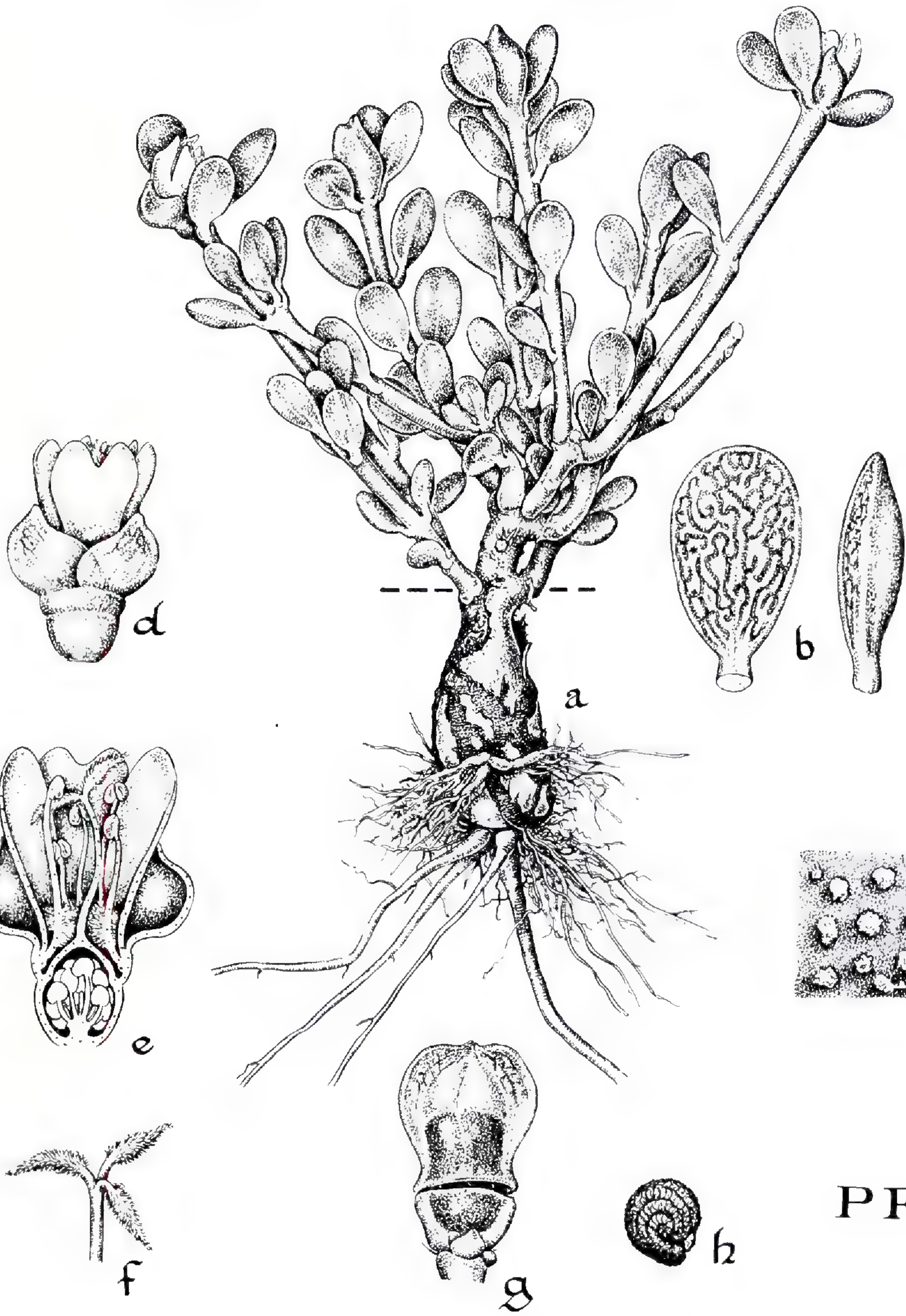

FIGURE 1. **Portulaca minuta:** a, habit, × 3; b, leaf, top and side views, showing pattern of chlorophyll-bearing cells just below surface of upper side of leaf, × 7; c, exudate from glands on surface of leaf, × 30; d, flower, natural position, × 6; e, flower, longitudinal section, × 9; f, stylar lobes, × 12; g, fruit, × 6; h, seed, × 18. *Drawn by Priscilla Fawcett.*

as petals, veiny. Petals 4, golden yellow, broadly obovate-cuneate, emarginate, about 3 mm. long. Stamens 8, irregular in length; filaments pubescent below middle. Stylar lobes 3, puberulent. Fruit about 3 mm. long

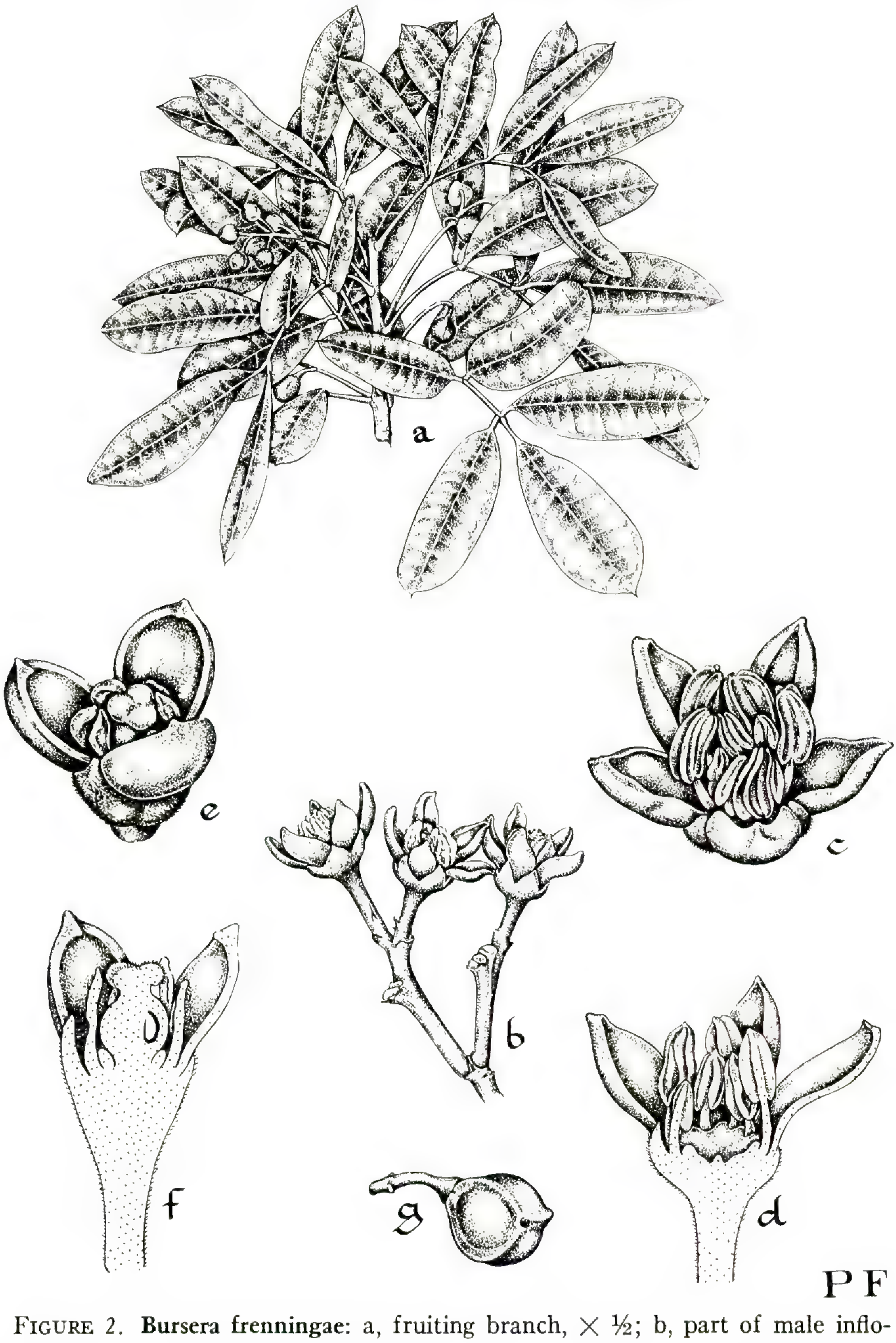

FIGURE 2. **Bursera frenningae**: a, fruiting branch, × ½; b, part of male inflorescence, × 3; c, male flower, natural position, × 9; d, male flower, longitudinal section, × 9; e, female flower, natural position, × 9; f, female flower, longitudinal section, × 9; g, fruit, × 1.5. *Drawn by Priscilla Fawcett.*

and 2 mm. wide, dehiscent below the middle to leave a cup 1 mm. deep, the cap miterlike. Seeds black, iridescent, pebbly, about 0.5 mm. across.

The abbreviated stems from a tuberous rootstock, opposite leaves, and three stylar lobes are distinctive features of this species.

BURSERACEAE

Bursera frenningae Correll, sp. nov. FIGURES 2, 3.

Frutex dioecious expansus, truncis multis, raro arbor parva, typice ramosissimus, cortice testacea vel rubiginosa, saepe aliquantum lamellata. Folia 3–5-foliolata (raro 7-foliolata); foliola crassichartacea, aliquantum late oblongo-elliptica vel elliptico-oblanceolata, rotundata vel obtusa saepe ad apicem apiculata, usque ad 5.5 cm. longa et 2.5 cm. lata. Inflorescentiae paniculas racemosas formantes; pedunculi florum masculorum multo longiores quam pedunculi florum femineorum; pedunculus fructus crassus et rigidus, raro plus quam 3 cm. longus; fructus suborbicularis, circa 7 mm. diametro.

TYPE. Bahamas. Great Exuma, in coastal rocky thicket between Mt. Thompson and Farmer's Hill, July 8, 1978, *D. S. Correll 49984* (A, holotype; F, FTG, NY, US, isotypes).

Multitrunked, dioecious, spreading shrubs or rarely small trees to about 4.5 meters tall, typically much branched, the bark reddish or reddish brown and often somewhat flaky; twigs with reddish brown bark. Leaves odd-pinnate; petiole to about 3 cm. long; blade to 7 cm. long; rachis commonly angularly arcuate. Leaflets 3 or 5, rarely 7, thick-chartaceous, rather broadly oblong-elliptic to elliptic-oblanceolate, rounded to obtuse and often apiculate at the apex, rounded to cuneate at the oblique base, 3–5.5 cm. long, 1.5–2.5 cm. wide; lateral leaflets subsessile to shortly petiolulate; terminal leaflet with a petiolule to about 1 cm. long. Inflorescences racemose-paniculate, 2.5–5 cm. long, puberulent, those of the male flowers much the longer; peduncle typically thick and rigid (especially in fruit), 1–3.5 cm. long; pedicels stout. *Male flowers* with pedicels 2–3 mm. long; calyx about 1 mm. long, with 5 minute, triangular lobes; petals 5, yellowish green, elliptic, obtuse to subacute, erect to erect-spreading, about 2 mm. long; stamens as many as 8. *Female flowers* with pedicels 1–1.5 mm. long; calyx 1–1.5 mm. long, with 3 rather broadly triangular lobes; petals 3, yellowish green, broadly elliptic, obtuse, erect to erect-spreading, about 2 mm. long and 1 mm. wide; infertile stamens usually 6; ovary sessile, with a sessile 3-lobed stigma; fruiting peduncle stout and rigid, rarely more than 3 cm. long; fruit with a pedicel about 3 mm. long, suborbicular, 3-celled, dehiscent, reddish brown, about 7 mm. long, bony.

This multitrunked, reddish-barked, usually shrubby plant has previously been included in the typically more southern *Bursera inaguensis* Britton. That small tree, however, characteristically has a solitary, often somewhat swollen trunk with tight, grayish bark. Its more slender petioles and peduncles are also much longer than those in our plant, and its leaflets are linear-oblong and somewhat acute.

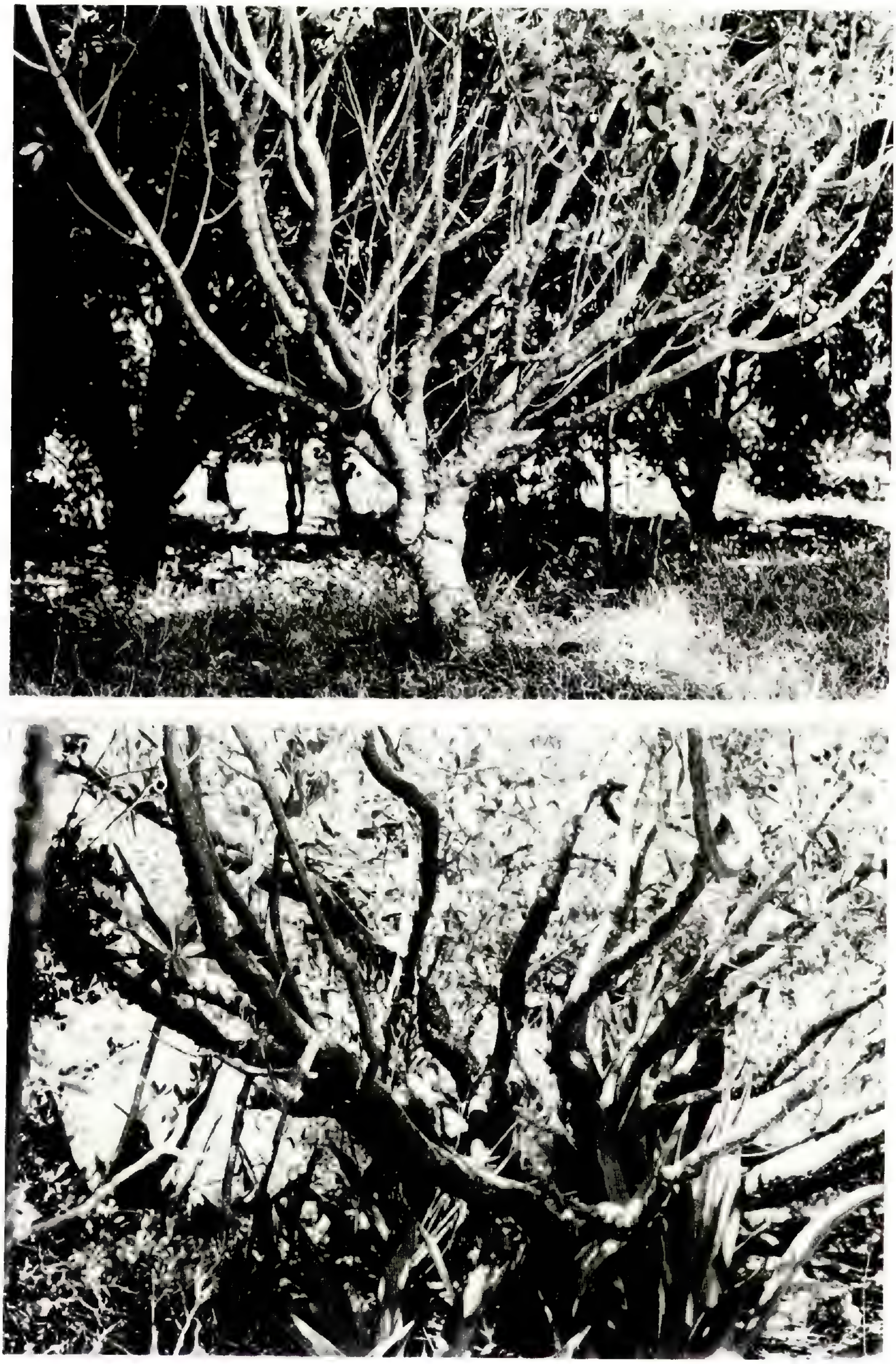

FIGURE 3. Above: **Bursera inaguensis,** dwarf tree from Great Inagua under cultivation at Fairchild Tropical Garden, showing gray-barked single trunk. Below: **Bursera frenningae,** shrub from type locality, showing numerous reddish-brown-barked stems arising from a common point of origin at ground level.

It is a pleasure to name this unique plant for Mrs. Blanche Borden Frenning, a favorite niece of the late Professor and Mrs. Oakes Ames, who were preeminent in the field of orchidology at Harvard University. Mrs. Frenning, a noted plantswoman in her own right, owns a home on Goat Cay, Great Exuma, where she has hospitably had my wife and me, as well as several of our botanical colleagues, as guests. Her generosity has thus made it possible for us to explore more intensively this rich segment of the Bahama Archipelago. We are, indeed, most grateful to Mrs. Frenning for her friendship and graciousness.

Tea made from the fresh leaves of gumbo-limbo or gum-elemi (*Bursera simaruba* (L.) Sarg.) is a refreshing drink. However, when I insisted on having tea made from the fresh leaves of *B. frenningae*, Jack Wright, who works for Mrs. Frenning, was appalled. Jack, whose hobby is carving boats, said that the tea would poison me and that when he once carved a boat from the wood it immediately sank to the bottom when placed in water. I did not drink enough of the tea to be poisoned, but what I did imbibe tasted like oily turpentine.

ADDITIONAL COLLECTIONS EXAMINED. **Cat Island:** in open coppice near Stevenson, *D. S. Correll 46150* (A, BM, F, FTG, IJ, MO, NY); on coppice-covered hills on north edge of Port Howe, *D. S. Correll 46222* (A, K, NY). **Great Exuma:** same location as holotype, *D. S. Correll 49927* (A, BM, F, FTG, IJ, K, MO, NY, US). **Long Island:** in coastal coppice on rolling hills north of Salt Pond, *D. S. Correll 48187* (A, DUKE, F, FTG, IJ, NY, TEX).

THEOPHRASTACEAE

Jacquinia berteri Sprengel var. nana Correll, var. nov.

Planta plus minusve 1 m. alta, a var. typica differt omnibus partibus minoribus, foliis oblanceolatis plerumque minus quam 2.5 cm. longis et 1 cm. latis, pedicellis gracilibus plerumque circa 5 mm. longis.

TYPE. Bahamas. Great Inagua, on edge of coppice southeast of road between Matthew Town and Morton Bahamas Ltd. headquarters, just east of Horse Pond; shrub about 1 meter tall, very dense; flowers greenish yellow, July 24, 1976, *D. S. Correll 47488* (A, holotype; BM, F, FTG, MO, NY, isotypes).

Plants 1 meter or less tall; leaves oblanceolate, mostly less than 2.5 cm. long and 1 cm. wide; pedicels slender, mostly about 5 mm. long.

Jacquinia keyensis Mez var. minutifolia Correll, var. nov.

Haec varietas a var. typica differt omnibus partibus minoribus, foliis elliptico-oblanceolatis vel spathulatis plerumque minus quam 2 cm. longis et circa 7 mm. latis, inflorescentia subtili, florum pedicellis gracilibus circa 7 mm. longis, calycibus 1.5 mm. longis.

TYPE. Bahamas. Great Inagua, scrubland at south end of the Salt Lake, July 7, 1963, *H. E. Hackett 202* (DUKE, holotype).

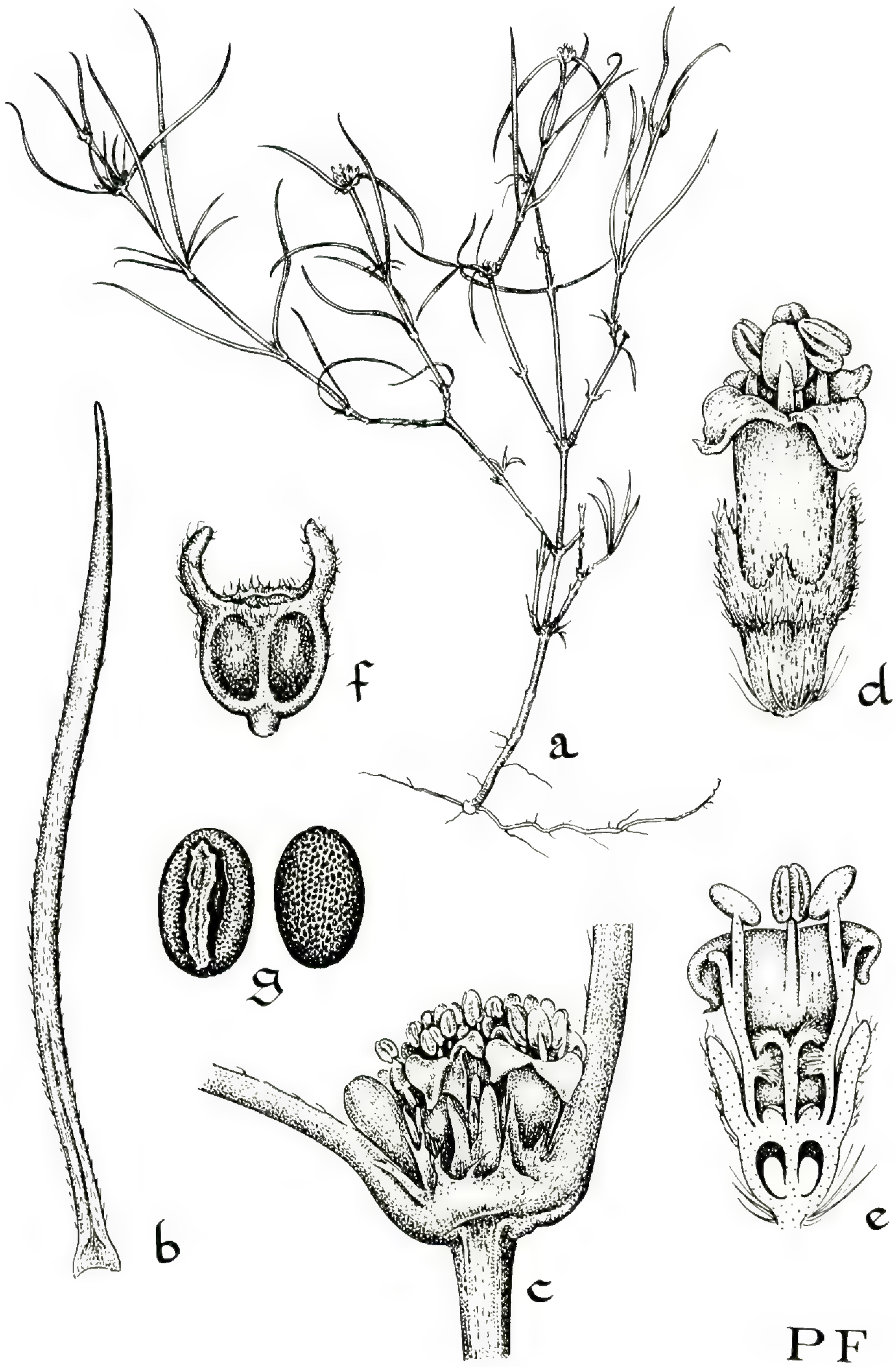

FIGURE 4. **Borreria capillaris:** a, habit, single stem from multistemmed plant, × ⅔; b, leaf, × 2; c, inflorescence, × 4; d, flower, natural position, × 12; e, flower, longitudinal section, × 12; f, fruit, × 6; g, seeds, ventral and dorsal views, × 16. *Drawn by Priscilla Fawcett.*

Leaves elliptic-oblanceolate to spatulate, mostly less than 2 cm. long and to about 7 mm. wide; inflorescence delicate; flowers with slender pedicels about 7 mm. long and calyces 1.5 mm. long.

Rubiaceae

Borreria capillaris Correll, sp. nov. FIGURE 4.

Herba succulenta, dense et intricate fruticosa, formam globularem faciens, caulibus filiformibus numerosis e radice gracile, usque 4 dm. alta et lata. Internodia plerumque ultra 2.5 cm. longa. Folia opposita, sessilia, filiformia, acuta, usque 5 cm. longa et 1 mm. lata, supra cum vel sine pubescentia adpressa. Flores in capitulis puberulis parvis plerumque minus quam 7 mm. latis e foliorum summorum axilis orti. Calyx puberulus, lobis subaequalibus 2 usque 4. Corolla alba guttis bruneolis; tubus circa 2 mm. longus, lobis 4 triangularibus effusis circa 0.5 mm. longis. Stamina 4, exserta. Semina nigra, ellipsoidea, margaritacea, muriculata.

TYPE. Caicos Islands. South Caicos, in thin soil on rock flats in somewhat open coppice on ridge between Cockburn Harbour and airport, soft balled shrubby plant; flowers white with brownish specks, February 11, 1978, *D. S. Correll 49942* (A, holotype; BM, F, FTG, IJ, MO, NY, TEX, US, isotypes).

Plant succulent, densely and intricately bushy to form a globular mass, with many filiform stems from a slender taproot, to about 4 dm. high and wide; internodes commonly 2.5 cm. or more long. Leaves opposite, sessile, filiform, acute, to about 5 cm. long and 1 mm. wide, with a prominent central vein on lower surface, with or without an appressed puberulence on upper surface. Flowers in small heads in upper leaf axils; heads puberulent, usually less than 7 mm. across. Calyx 1.5–2 mm. long, puberulent, with 2 to 4 subequal subulate lobes that are somewhat shorter than the body. Corolla white with brownish specks; tube about 2 mm. long, with 4 triangular spreading lobes about 0.5 mm. long. Stamens 4, exserted. Seeds black, iridescent, pebbled, ellipsoid, about 1 mm. long.

This species grows in the proximity of the recently discovered *Oxalis eggersii* Urban (*Correll 49284*), new to our flora. When growing, the uniformly filiform, succulent, entangled leaves and branches of the plant resemble a ball of hair.

The nearest species with which our plant can be compared is the usually robust *Borreria savannarum* Britton of Great Inagua. It differs from that species, however, in its delicate, slender, succulent stems and leaves.

ACKNOWLEDGMENTS

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and Turks Islands. The excellent drawings are those of Miss Priscilla Fawcett, Staff Artist of the Fairchild Tropical Garden, to whom I am most grateful. I also wish to thank my wife, Dr. Helen B. Correll, for her contributions to my research, and also those individuals in the islands who have contributed much toward making my field explorations more successful than they would have been otherwise. I wish to acknowledge the assistance of Dennis Wm. Stevenson with the photographs.

FAIRCHILD TROPICAL GARDEN
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SYSTEMATIC ANATOMY OF BAHAMIAN SPECIES OF BURSERA (BURSERACEAE)

DENNIS WM. STEVENSON

AS A RESULT of his work on the flora of the Bahamas and Turks and Caicos Islands, Donovan S. Correll (1979) has recognized three species of *Bursera*. He has described a new species, *B. frenningae*, as distinct from *B. simaruba* and *B. inaguensis*. The identification of these three taxa is presently based on qualitative morphological characters that can frequently vary.

The systematic anatomy of the Burseraceae has been described by Metcalfe and Chalk (1950, and the references cited therein). Webber (1941), Heimsch (1942), and Metcalfe and Chalk (1950) report on the apparent anatomical homogeneity of this family. For example, the vessels of the secondary xylem invariably have simple perforation plates and hexagonal-bordered pits, and the presence of resin canals in the secondary phloem is considered to be diagnostic for the family (Metcalfe & Chalk, 1950; Brizicky, 1962).

On the other hand, features such as thick- vs. thin-walled fibers have been found to be useful in segregating taxa at the generic level within the Burseraceae (Metcalfe & Chalk, 1950). Because of this, I hoped that supportive characters might be found in the stem anatomy that would further aid in the separation of these plants. I also thought that it might reveal the relationship of these three taxa.

Included in Correll's collections for propagation in the Bahamian collection at the Fairchild Tropical Garden are living stem pieces of two of the species; the third species is already under cultivation there. Radial, tangential, and transverse sections were cut from equivalent-sized stem pieces of *Bursera simaruba* (*Correll 49986*), *B. frenningae* (*Correll 49984*), and *B. inaguensis* (*Stevenson 448*). Voucher specimens bearing these collection numbers have been deposited in the FTG herbarium.

Subsequent examination of this material showed both similarities and differences. Some of these similarities revealed are in the wood structure: for example, all three taxa have diffuse porous wood composed of vessels with simple perforation plates and alternate hexagonal-bordered pitting, heterogeneous rays, numerous tyloses, and simple-pitted septate fibers. Vessel length is also fairly uniform (TABLE 1) among all three taxa.

However, the three taxa do have certain structural differences. Examination revealed that *Bursera simaruba* has an average vessel diameter of about 74 μm. (TABLE 1), a high percentage of biseriate rays (TABLE 2), resin canals and oil cells randomly arranged within the secondary phloem, and, of diagnostic importance, secondary phloem fibers.

Bursera inaguensis, on the other hand, has an average vessel diameter of about 60 μm., a very high percentage of biseriate rays, and, of diagnostic importance, resin canals arranged in obvious circumferential rings within the secondary phloem. *Bursera inaguensis*, in contrast to *B. simaruba*, does not have secondary phloem fibers.

TABLE 1. **Vessel diameter and length in three species of Bursera.***

	RANGE	MEAN	S.D.
	Diameter		
B. simaruba	45–108	73.8	13.4
B. inaguensis	36–78	59.6	11.7
B. frenningae	24–75	43.7	11.5
	Length		
B. simaruba	180–350	260.6	49.4
B. inaguensis	210–360	273.0	45.4
B. frenningae	180–400	287.2	43.7

* Measurements given in μm.

TABLE 2. **Ray type in three species of Bursera.**

	BISERIATE	TRISERIATE
B. simaruba	110 (80%)	26 (20%)
B. inaguensis	130 (96%)	6 (4%)
B. frenningae	69 (51%)	67 (49%)

Finally, examination revealed that *Bursera frenningae* has a mean vessel diameter of about 44 μm., a characteristically low percentage of biseriate rays (thus, a correspondingly high percentage of triseriate rays), and randomly arranged resin canals and oil cells in the secondary phloem; it also lacks secondary phloem fibers.

In summary, *Bursera simaruba* has vessels that are significantly larger in diameter than those of *B. frenningae* (which has the smallest vessel diameter), whereas *B. inaguensis* has intermediate-sized vessels. *Bursera frenningae* not only has the smallest vessel diameter, but also contains significantly higher percentages of triseriate rays than do the other two species. *Bursera simaruba* is the only taxon of the three that has fibers in the secondary phloem. While all three taxa have oil cells and resin canals within the secondary phloem, only *B. inaguensis* has these structures arranged in concentric, circumferential rings.

These various stem characters, all of which can be observed by using razor blade sections and a dissecting microscope, can be readily utilized to key out the three species as follows:

Key to Bahamian Species of Bursera Based on Anatomical Characteristics

1. Phloem fibers present in the secondary phloem. ..... *B. simaruba.*
1. Phloem fibers not present in the secondary phloem.
   2. Oil cells and resin canals arranged in concentric, circumferential rings within the secondary phloem. ..... *B. inaguensis.*
   2. Oil cells and resin canals arranged randomly within the secondary phloem. ..... B. *frenningae.*

Thus, comparative stem anatomy fully supports Correll's (1979) recognition of three species of *Bursera* in the Bahamas and Turks and Caicos Islands. On anatomical as well as systematic grounds, *Bursera frenningae* is recognized as a new and distinct taxon.

ACKNOWLEDGMENTS

I thank Dr. Donovan S. Correll for supplying materials used in this study and, more importantly, for his advice and encouragement. I deeply appreciate the editorial assistance of Ms. Janice Wassmer.

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Journal of the Arnold Arboretum *January, 1979*

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COVER: The buds, leaves, and fruit of *Carpinus caroliniana* Walter, hornbeam or blue beech, form the basis of this year's cover design. An individual nutlet, together with its leafy, three-lobed wing, will appear on the offprints; a series of these was used in designing the device that appears on the back cover. The designs were all drawn by Karen Stoutsenberger from materials collected from plants growing in the Arnold Arboretum.

Widespread in the Northern Hemisphere, *Carpinus* L. (placed in the Betulaceae or alternatively in the Corylaceae or even the Carpinaceae), with upwards of 35 species, exhibits a disrupted Arcto-Tertiary distribution in eastern North America, Europe, Asia Minor, and in eastern Asia where the center of species diversity occurs. The only North American representative of the genus, *C. caroliniana* grows along the edges of streams and in wet, rich soils in forested areas from Nova Scotia and Quebec southward to Florida and westward into Minnesota, Iowa, Missouri, eastern Texas, and Oklahoma. Disjunct populations are known in mountainous regions of southern Mexico and in Central America.

The stems of *Carpinus caroliniana*, a small tree, have smooth, brownish- or bluish-gray, sinuate bark and an appearance reminiscent of those of beech trees (*Fagus* spp.). The wood, which is occasionally used for tool handles, is light brown to nearly white. Its growth habit, relatively small size, conspicuous infructescences, and foliage, which turns deep scarlet and orange to yellow in fall, combine to make this species an attractive native ornamental. — *S. A. S.*

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BOREAL AND WESTERN NORTH AMERICAN PLANTS IN THE LATE PLEISTOCENE OF VERMONT [1]

NORTON G. MILLER AND GARY G. THOMPSON

MOST QUATERNARY PALEOBOTANICAL STUDIES are aimed at determining floristic composition and vegetation types, and from these, by inference, climates and other environmental features of the past. In North America little use has been made of the Pleistocene and Holocene fossil plant record to explain development of distribution patterns of plants other than trees. No doubt this is because fully identified megascopic plant remains are known from relatively few localities when compared with Britain and northern parts of Europe, for which there are admirable syntheses of historical phytogeography based on fossils (e.g., Godwin, 1975).

We report here on a reinvestigation of fossiliferous lake sediments that contain many phytogeographically noteworthy species. The deposit is located in the upper Connecticut River valley near Colebrook, New Hampshire, and was discovered in the late 1920's by R. J. Lougee. Arthur Hollick (1931) treated plant fossils from the deposit in one of the first detailed reports of a North American late glacial leaf flora. Unfortunately, Hollick's specimens came from oxidized layers that contain only poorly preserved macrofossils. Our digging uncovered deeper, organic-rich lenses of unoxidized plant materials among which were wood fragments in sufficient quantity for radiocarbon dating. Pollen and spores were also found to be present throughout the section. This new material has permitted confirmation or revision of Hollick's determinations and an interpretation of the late glacial environment based on both pollen and plant macrofossils.

Megascopic Quaternary plant fossils have been reported from a few other places in New England. At sites near Hadley and Amherst, Massachusetts, in lake clays in the Connecticut River valley, Emerson (1898)

[1] We dedicate this paper to Stanley Jay Smith (20 September 1915–20 July 1978), Curator of Botany at the New York State Museum, ardent field botanist, and longtime student of the eastern North American flora and its geographic relationships.

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noted leaves and fruits of several species of arctic-alpine flowering plants. More recently, Ashley (1972) reported fossil leaves (including a specimen identified as *Vaccinium ?uliginosum* L.) in clays of glacial Lake Hitchcock from several places in Massachusetts and Connecticut. Fossils of arctic and alpine plants, most notably *Salix herbacea* L. and *Dryas integrifolia* Vahl, have also been found in late glacial clays at Cambridge, Massachusetts (Argus & Davis, 1962). The flora reported by Hollick (1931) differed from these, however, in containing leaves of trees. Our new fossil assemblages show that trees (balsam poplar and spruce) indeed occurred near the site, but that surfaces were mostly covered by an open vegetation of herbs and low woody plants intolerant of shade.

Among the terrestrial plants listed by Hollick (1931), we confirm the presence of *Populus balsamifera* L., *Dryas Drummondii* Richardson, and possibly *Salix argyrocarpa* Andersson and/or *S. pellita* Andersson, but we found no specimens of *S. pedicellaris* Pursh or *Vaccinium angustifolium* Aiton. Previously unrecognized species are added to the flora, and revisions are suggested for Hollick's material of *Salix reticulata* L., *Celtis occidentalis* L., *Loiseleuria procumbens* (L.) Desv., *Kalmia polifolia* Wangenh., and *Vaccinium macrocarpon* Aiton. Some of the species represented by fossils now have an eastern-western North American disjunct distribution. The fossils establish that such present-day disjuncts once grew in eastern North America south of their present areas of occurrence. Furthermore, they grew at low elevations on surfaces that had been recently freed of glacial ice.

GEOLOGIC SETTING

Regional Description and Glacial History

The plant fossils occur in sediments exposed on the west bank of the Connecticut River in Lemington Township, Essex County, Vermont (Figure 1). The fossil locality, which we designate the Columbia Bridge Site, is at lat. 44°50′50″ N., long. 70°38′30″ W., 0.8 km. south of the Columbia Bridge (a wooden covered bridge). The site is at an elevation of 301 meters in the Northeastern Highlands of Vermont, a northwestern extension of the White Mountains of New Hampshire (Fenneman, 1938; Jacobs, 1950). Relief is high, with Monadnock Mountain (elev. 957 m.) just 4 km. north of the site. Metamorphic rocks (chlorite- to sillimanite-grade metasediments) underlie most of the area (Myers, 1964).

A thin, discontinuous mantle of till is spread over the uplands near the site. Thicknesses are generally less than 7 meters, in contrast to those in valleys, where till over 30 meters thick has been measured (Stewart & MacClintock, 1969). Stewart and MacClintock (1969) reported two types of till in the region. One is a "dense, compact till," with more erratic fragmental material than the second, which has a higher percentage of local bedrock fragments.

On the basis of till fabric, Stewart and MacClintock (1969) recognize

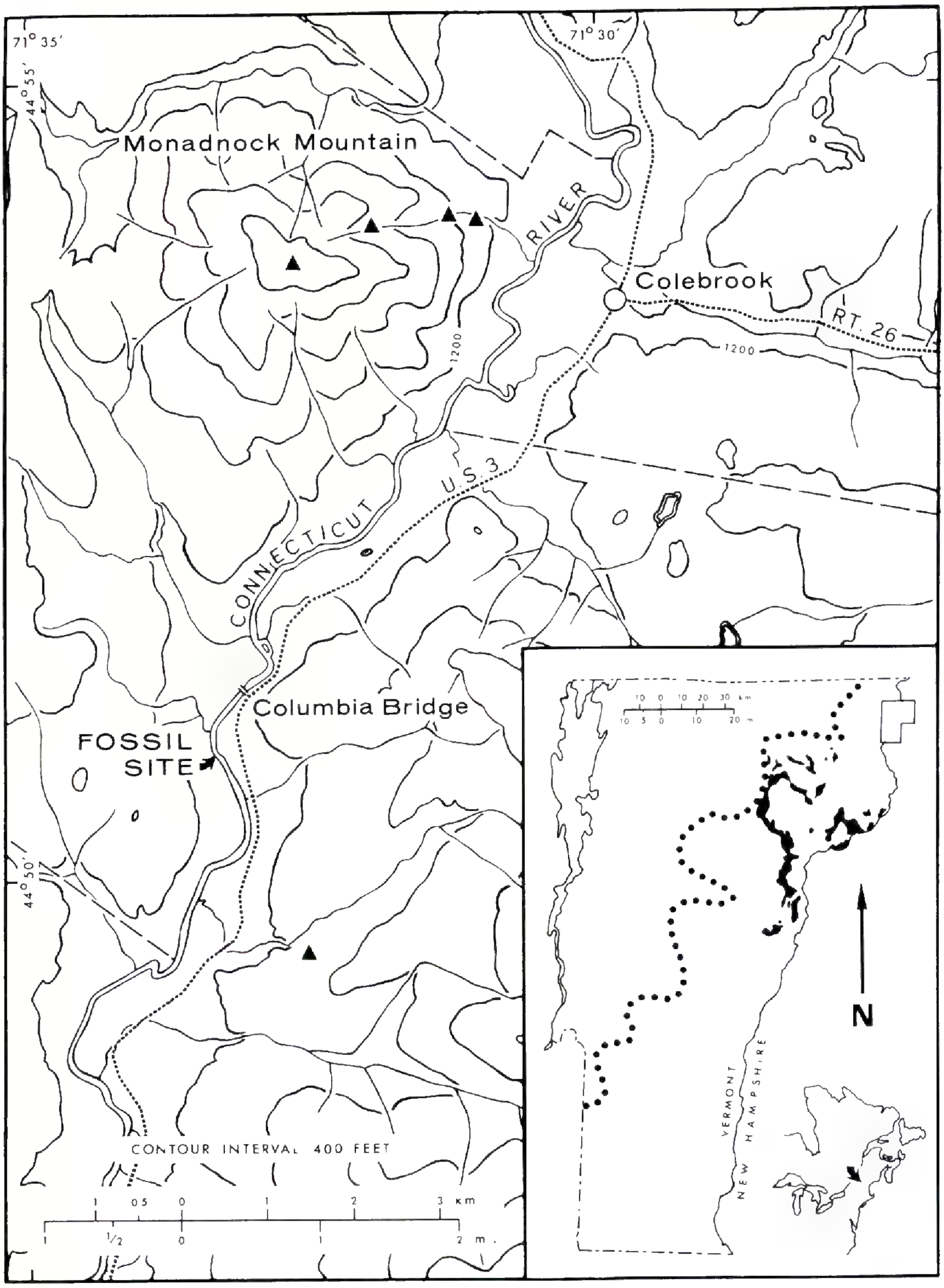

FIGURE 1. Topographic map of upper Connecticut River valley showing location of Columbia Bridge site and places where surface pollen samples were obtained (black triangles). Inset: map of Vermont, kame moraines of Shelburne drift in black, Burlington drift border dotted, area of large scale map outlined. (Topographic base from U.S.G.S. Averill, Vermont-New Hampshire, and Dixville, New Hampshire, 15 min. quadrangles; inset map after Stewart & MacClintock, 1969.)

two tills of Wisconsinan age in the region: the Bennington (older), with a northwest–southeast fabric; and the Shelburne (younger), with a northeast–southwest fabric. A third, still younger till, the Burlington, with a northwest–southeast fabric, is recognized to the west of the area. Stewart and MacClintock have concluded that till fabric, as measured by their technique, shows ice-flow direction. Other evidence from Vermont (Flint, 1971, p. 178; Larsen, 1975; Wagner *et al.*, 1972) indicates that ice did not flow as Stewart and MacClintock have postulated, therefore the reality of the Bennington, Shelburne, and Burlington tills is controversial. Stewart and MacClintock interpret the Connecticut Valley glaciolacustrine sediments as having been deposited with the northward retreat of the Shelburne ice margin. They interpret landforms in the vicinity of St. Johnsbury, Vermont (FIGURE 1), as possibly being recessional moraines formed by Shelburne ice.

In Quebec, south of the St. Lawrence River, a sequence of dated moraines 12,800 to 11,000 years old (Gadd *et al.*, 1972) marks the retreat of the margin of the last glacier north of the Columbia Bridge site. Carbon-14 ages for the Champlain Sea, which occupied the St. Lawrence River and Champlain valleys, range from about 12,500 to 10,000 years B.P. (Cronin, 1977). Events reflected in Quebec may correlate with retreat of the Burlington ice in Vermont, although there are no supporting carbon-14 dates from Vermont where the ice margin position is marked by poorly developed moraines only (FIGURE 1; Stewart & MacClintock, 1969).

The chronology and process by which the continental glacier retreated from New England is still debated. Active zone retreat is indicated by recessional moraines and deformed sediment produced as a result of ice readvance, but few such features are found in northern Vermont. Stagnation zone retreat accounts for ice-contact features and an absence of recessional moraines. Recent data from Connecticut indicate an active ice margin in the Connecticut Valley (Larsen, 1978). Stone and Koteff (1973) interpret evidence in the Merrimac Valley, New Hampshire, as indicating active zone retreat, which Caldwell *et al.* (1978) have indirectly dated at about 13,500 years B.P. About 140 km. north of the locality of Caldwell *et al.*, an age of over 13,000 years has been reported recently from a lake basin on the flank of Mount Washington in the White Mountains (Spear, 1978).

As ice disappeared from New England, by whatever mechanism, lakes were dammed in valleys by the remaining ice or by drift deposited from it. The Connecticut Valley, being a main water course, contained large proglacial lakes. Lake Hitchcock, the largest and best documented of these, extended from a till dam at Rocky Hill, Connecticut, to Lyme, New Hampshire (Schafer & Hartshorn, 1965). North of Lake Hitchcock, and presumably younger, although less well documented, were Lakes Upham, Coös, and Colebrook (Lougee, 1939). Radiocarbon-dated pollen profiles from Connecticut bogs suggest a glacial readvance in southern New England shortly before 13,000 years B.P. (Flint, 1956). The date of Lake Hitchcock drainage, inferred from two carbon-14 age determinations, is

about 10,700 years B.P. (Flint, 1956), implying that Lake Hitchcock lasted 2000 to 3000 years. Antevs (1922), who worked out a varve record in Lake Hitchcock sediment of over 4000 years, inferred a much longer existence for the lake (see also Verosub, 1975). Prior to those reported in this paper, no carbon-14 dates had been directly determined from any lake sediment in the Connecticut Valley, nor have there been any radiocarbon dates that relate to the presumed younger lakes. The Columbia Bridge site is within the area of Lake Colebrook.

At Columbia Bridge the Connecticut Valley is narrow (0.6 km. wide), with relatively steep bedrock walls. Upstream from the site, along the flank of Monadnock Mountain, the valley is choked with high relief drift, and the river channel is restricted. This drift may have dammed a lake in the valley. Along the valley throughout this area is a complex arrangement of sediments and landforms which have been interpreted as deltas, beaches, kame terraces, eskers, and recent alluvium (Cannon, 1964; Stewart & MacClintock, 1970). Because lithologies composing these landforms may be similar and because there is no age control, we feel that a more detailed study of the surficial geology is required before the history of the valley lakes and river in this segment of the valley can be known. Such an interpretation is beyond the scope of this study.

Description and Interpretation of Sediments

Lake sediment and alluvium crop out at the fossil site over an area of about 25 square meters where at least 3.5 meters of rhythmically laminated fossiliferous silt, sand, and clay is overlain by 4 meters of sand and silt. The lateral extent of the sediments is known in detail only within several meters of the exposure as a result of hand augering.

Sediments in the upper 4 meters grade uniformly from a basal orange to reddish brown, pebbly, coarse sand (with widely separated cobbles at the bottom) to light brownish yellow silt at the top. This upper unit contains small- and medium-scale cross laminations, which indicate current directions paralleling the crests of swells and the troughs of swales on the floodplain at the site. Thickness, particle size distribution, and current directions indicate that this unit is a recent point bar deposit. This deposit unconformably overlies the laminated unit, with an irregular contact. There is no evidence of how much laminated sediment was eroded before the deposition of the overlying sand unit.

The rhythmically laminated unit consists of alternating coarse and fine laminae. Fine-grained laminae range in thickness from 0.05 to 3.36 cm. ($\overline{X}$ 0.77 cm., s.d. 0.65); coarse-grained laminae from 0.08 to 3.48 cm. ($\overline{X}$ 0.64 cm., s.d. 0.57). The average couplet thickness is 1.39 cm. Pipette analysis of one fine-grained lamina revealed a mean grain size of 6.6 ϕ and a clay content of about 25 percent. This is coarser than the fine laminae of rhythmites in Lake Hitchcock sediments (Ashley, 1972). Coarse-grained laminae consist of silt and sand, with some exhibiting ripple cross-laminations. The clay-rich laminae are medium gray; silt and sand laminae

are light brownish yellow, except in the oxidized upper 0.75 meter, where the fine ones are light brownish yellow and the coarse ones reddish brown. Pebbles and one boulder (30 × 21 × 12 cm.) were found widely spaced in the sediment. These are interpreted as dropstones from floating ice laden with coarse sediment.

We are unable to conclude definitely that all the rhythmites are varves. As is common among varves, many of the contacts between silt or sand and clayey silt beneath are sharp. Graded fine-grained laminae are known among summer layers attributed to spasmodic turbidity currents (Ashley, 1972). Among the Columbia Bridge rhythmites there are no megascopically obvious graded laminae, and a detailed pipette analysis showed no grading. On the other hand, winter layers tend to be of uniform thickness and grading throughout a sequence (Ashley, 1972). At Columbia Bridge the thickness of the fine-grained laminae is variable, and many of them contain thinner, coarse-grained laminae, making it difficult to recognize a winter layer. Although it is not possible to match such rhythmites with a varve category recognized by Ashley (1972) for Lake Hitchcock sediments, particle size data and the variation in lamina thickness compare most closely with her type II varves.

While it was difficult to count the number of couplets accurately, our best estimate is 116 between 0 and 1.65 meters. Fortuitous as it may be, radiocarbon dating of the interval 0.84–1.58 meters, which contains 66 couplets, indicates that as few as 75 or as many as 375 years may separate the dated levels. Thus, it is possible that paired laminae represent annual accumulations of sediment.

The laminated sediments are deformed. In the upper meter the laminae dip 15° south 84° west, and the uppermost are truncated at the unconformity. A few normal faults were seen in the exposure, and the strike of one of these was approximately north–south, with a dip to the east of about 45°. The faults did not pass into the sand unit above. The deformation is possibly related to slumping. Although the overlying sand unit has slumped along the present river bank, there is no conclusive evidence that the laminated sediment has slumped recently. The deformation appears to represent collapse that resulted when a supporting ice mass melted. This suggests that the sediments are ice-contact lake deposits.

Plant detritus is concentrated in sandy lenses a few mm. thick and a few dm. wide throughout the exposed laminated sediments. In approximately the upper 0.75 meter, megascopic plant remains have been largely replaced by limonite(?). Below this level plant materials are essentially unaltered, and well-preserved fossils were recovered. The lenses of whole and fragmented plant remains are interpreted as concentrations of waterlogged litter that has been transported from the shore or by inflowing streams into deep water through the action of turbidity currents and deposited with silt and sand. Because these lenses occur throughout the section, having been deposited frequently over many years, they represent a common depositional phenomenon in the lake.

Leaves of the rooted aquatic *Potamogeton* occur in fine as well as coarse

laminae below the oxidized zone. Some leaves are oriented more or less vertically as if buried slowly in the position of growth. The leaf surface is commonly coated with a thin layer of calcium carbonate. These plants existed in water that was clear and warm enough to support their growth.

PRESENT VEGETATION

Slopes on the west and east sides of the Connecticut River valley near Columbia Bridge support forest of the hemlock-northern hardwood type. Balsam fir (*Abies balsamea* (L.) Miller) and red spruce (*Picea rubens* Sarg.) occur sparsely intermixed or in more abundance on abandoned cleared land and near the summit of Monadnock Mountain. Selective logging was apparent in all visited stands except those at higher elevations. Much of the valley floor and adjacent lower slopes is nonforest land.

Moss polsters for pollen analysis were collected at four elevations on the east slope of Monadnock Mountain along the trail to its summit, and at one place on the west flank of Jordan Hill, which is southeast of Columbia Bridge (FIGURE 1). Notes were taken on forest composition around the collecting sites, but no detailed inventory was undertaken. Birches (*Betula alleghaniensis* Britton, *B. papyrifera* Marsh.) and sugar maple (*Acer saccharum* Marsh.) were frequent at all elevations except near the top of Monadnock Mountain, where balsam fir was abundant. Hemlock (*Tsuga canadensis* (L.) Carr.) and beech (*Fagus grandifolia* Ehrh.) were encountered in small amounts at low and middle elevations on the east flank of Monadnock Mountain.

Surface pollen assemblages (TABLE 1) are dominated by birch, and contributions of diverse trees and shrubs (in low percentages) account for the remainder of the arboreal component. Pollen of herbs is 9 percent or less. Fir pollen is most abundant in the sample collected just below the summit of Monadnock Mountain. Other differences in the spectra that relate to elevation are also apparent. When compared with those from surface lake muds at Brownington Pond, 47 km. to the west (Davis & Goodlett, 1960), the spectra agree in high birch and low oak values but differ in having lower percentages of beech and hemlock.

METHODS

Samples were collected at the fossil site in October, 1976, February, 1977, and January, 1978. The lake sediments were located by digging through slumped material at the locality described and illustrated by Hollick (1931) and Lougee (1939). Because the fossiliferous sediments were near river level, we could sample them only at low water. The surface was cleaned, and, to sample as deeply as possible, a vertical pit approximately 45 $\times$ 60 cm. was dug to a depth of 1.65 meters into the lake sediments below river level. In January, 1978, a second pit was dug to 1.76 meters to recover additional material for carbon-14 analysis.

For macrofossils and for carbon-14 analysis, blocks of sediment were

TABLE 1. **Pollen assemblages from moss polsters, Columbia Bridge area, upper Connecticut River valley, northern Vermont–New Hampshire.**

Sample No.	1*	2*	3*	4*	5†
Elevation (meters)	955	670	455	395	410
Trees, shrubs, herbs ‡					
Picea	1.0%	6.0%	5.7%	8.3%	4.4%
Abies	12.7	2.5	2.3	3.5	2.8
Pinus	3.9	1.5	2.0	6.1	5.2
Tsuga	0.8	—	0.9	0.6	1.1
Fagus	1.6	0.6	1.0	1.5	1.1
Acer saccharum	3.2	4.5	2.2	14.1	5.1
Fraxinus 4-colpate	1.8	0.4	0.3	0.1	1.7
Juglans	—	—	0.1	—	—
Carya	—	0.1	—	—	—
Quercus	3.4	1.2	2.0	1.0	1.0
Ulmus	1.6	0.1	0.1	0.4	0.2
Fraxinus 3-colpate	0.5	—	0.2	0.2	1.2
Acer rubrum	0.5	0.6	0.3	0.1	1.2
Betula	58.9	72.5	62.6	50.3	65.7
Carpinus-Ostrya	0.3	0.4	—	1.5	0.1
Populus	—	0.1	—	0.1	—
Juniperus-Thuja	—	—	0.1	0.4	0.3
Alnus	1.1	0.7	0.7	0.8	0.9
Salix	0.2	—	0.1	0.1	0.1
Acer spicatum	0.5	4.9	14.4	1.4	0.6
Corylus	0.2	—	—	0.1	0.1
Cyperaceae	0.2	0.1	—	—	—
Gramineae	1.0	0.8	1.4	4.8	2.5
Ambrosia	6.1	1.3	2.4	3.6	3.1
Rumex	—	0.1	—	0.1	0.3
Plantago	—	0.4	0.1	—	—
Chenopodiaceae-Amaranthaceae	0.2	—	—	0.1	0.4
High-spine Compositae	0.3	0.4	0.8	0.3	0.7
Ranunculus	0.2	0.1	—	—	—
Coptis	—	—	0.1	—	—
Sum AP	92.1	96.4	95.2	91.0	92.9
Sum NAP	7.9	3.6	4.8	9.0	7.1
Miscellaneous §					
Polypodiaceae	27.7	12.2	8.7	10.5	33.0
Lycopodiaceae	0.2	0.2	—	0.1	0.6
Osmundaceae	—	—	—	0.1	—
Ophioglossaceae	0.1	0.1	—	—	—
Typha-Sparganium	—	—	—	0.2	—
Broken Abietineae	2.3	0.8	1.4	1.4	1.7
Unfamiliar	0.1	0.1	—	0.3	0.1
Unknown	1.9	1.5	5.7	2.2	2.2

* Samples from east slope of Monadnock Mountain, Essex County, Vermont.
† Sample from west slope of Jordan Hill, Coös County, New Hampshire.
‡ Percentage base = sum AP + NAP.
§ Percentage base = sum AP + NAP + sum miscellaneous.

cut from the pit at those levels where lenses of organic detritus were concentrated. These were wrapped in aluminum foil for transport. In the laboratory the blocks were teased apart, and plant-bearing horizons were washed with tap water through a 500 μm. sieve. Residues were examined under a dissecting microscope. For two of the carbon-14 analyses (WIS-919 and WIS-961), detrital wood fragments (ca. 4.5 g. dry weight) were picked from the residues under a dissecting microscope. For WIS-925, a sediment block rich in organic detritus was submitted. Carbon-14 analyses were made by the Radiocarbon Laboratory, Center for Climatic Research, University of Wisconsin, Madison.

Sediment samples for pollen analysis were cut from a fresh vertical wall of the pit in 5 cm. lengths of triangular cross section (ca. 5 cm. along a side). In the laboratory a 4 cc. subsample was removed from across the full length of selected segments after the exposed sediment had first been chipped away. In an unsuccessful attempt to determine total depth by augering and probing, the laminated sediment was penetrated to 3.59 meters. Sediments between 3.49 and 3.59 meters were collected in a Davis sampler head. Subsamples from this short core, which was 1.89 meters below the next sample above, were combined for pollen analysis.

Subsamples were macerated in 10 percent hydrochloric acid and 70 percent hydrofluoric acid, and the residues were sieved followed by flotation in zinc chloride solution (sp. gr. 2.0). Residues with excessive organic matter were acetolyzed. Glycerine jelly was the mounting medium.

Concentrating the pollen and spores, which occurred in low densities in the sediments, was facilitated by washing extraneous materials through a screen with 10 μm. openings. Unsieved residues were diluted with large amounts of fine silt- and clay-sized particles that made tabulation of the pollen and spores time-consuming and impractical. Fine-grained, insoluble, opaque particles of unknown composition were especially troublesome. Nitex Monofilament Nylon Screen HC (high capacity) 3–10 (available from TETKO, Inc., Elmsford, New York 10523) was used. After treating a sample with acids, the residue was washed with distilled water through the screen. The sieving apparatus consisted of a cylindrical plastic freezer container with the flat bottom and all but the rim of the lid cut away. A square piece of screen was placed over the top of the container and clamped tightly in place with the lid-rim, which extended above the taut screen. A residue was washed onto the screen after the apparatus was suspended by its rim in a beaker. The complete apparatus was vibrated on an electromagnetic sieve shaker, and water was added from a wash bottle until only clean water moved through the screen. The screen was then removed, and the residue was washed into a beaker with repeated jets from a wash bottle. The screen was examined under a microscope for adhering particles and, if necessary, washed again. The residue was concentrated by centrifuging. No pollen grains were detected in the sediment that passed through the screen. Also, a few unscreened samples were laboriously counted and compared with spectra from screened duplicate samples. Pollen assemblages obtained from the same depth by both methods were similar, and we concluded that little, if any, pollen found its

way through the screen. We were able to recover pollen in concentrations of less than 100 grains per cc. of sediment.

For determination of pollen concentration, separate subsamples, each consisting of 2.5 cc. of sediment from across a single rhythmite, were taken at evenly spaced intervals through the section. The moist sediment was measured by pressing it into a 1.25 cc. measuring spoon. These subsamples were treated like the others (although none was acetolyzed), and the residues were placed in glycerine jelly. A residue-fraction was determined by first counting the number of drops of liquid glycerine jelly containing the residue, then placing one or two drops on a microscope slide after completely mixing the residue with a pumping action of the pipette and bulb. If it is assumed that each rhythmite is a yearly increment, then the number of pollen and spores per cubic centimeter (total number in a residue divided by 2.5) multiplied by the varve thickness equals the number of pollen and spores deposited per $cm.^2$ per year (i.e., pollen influx).

The residues were counted at a magnification of 200×. Microscope slides were traversed according to a prescribed plan to prevent overlap and insure randomness. Except where density was too low, each sample was counted until a sum of 300 arboreal and shrub pollen grains was reached. A collection of modern pollen consisting of about 10,000 slides and broadly representing the flora of North America was routinely used for reference purposes. Pollen of *Dryas Drummondii* Richardson, a species represented in the deposit by abundant macrofossils, proved upon careful examination to be different from that of other *Dryas* species. It sometimes appeared scabrate (pollen grains were in various stages of development on the reference slides) and with no alignment of elements to produce rugulae or striae. Thus, especially when slightly degraded, pollen of *D. Drummondii* can appear much like that of *Quercus*. However, after rechecking all grains doubtfully identified as *Quercus*, we found only one or possibly two that we concluded might be of *D. Drummondii*.

To measure the present-day pollen rain in the vicinity of the fossil site, several samples of moss polsters were analyzed. Tips of the moss plants were cut off and acetolyzed, and the residues were sieved through fine metal screening. The pollen residues were counted like the others.

Both fossil and modern seeds received two coatings of gold-palladium (total thickness 250 Å), preceded by an optional coating of carbon, prior to examination with a scanning electron microscope (AMR Model 1000). Fully mature seeds of representative form were selected for SEM study after examination of seeds from at least two different herbarium specimens of each species.

RESULTS

POLLEN ANALYSES

Except for minor pollen and spore types, which are listed in APPENDIX A, results of the pollen analysis are displayed in FIGURE 2. The scale at the left of the diagram represents depth below the top of the laminated

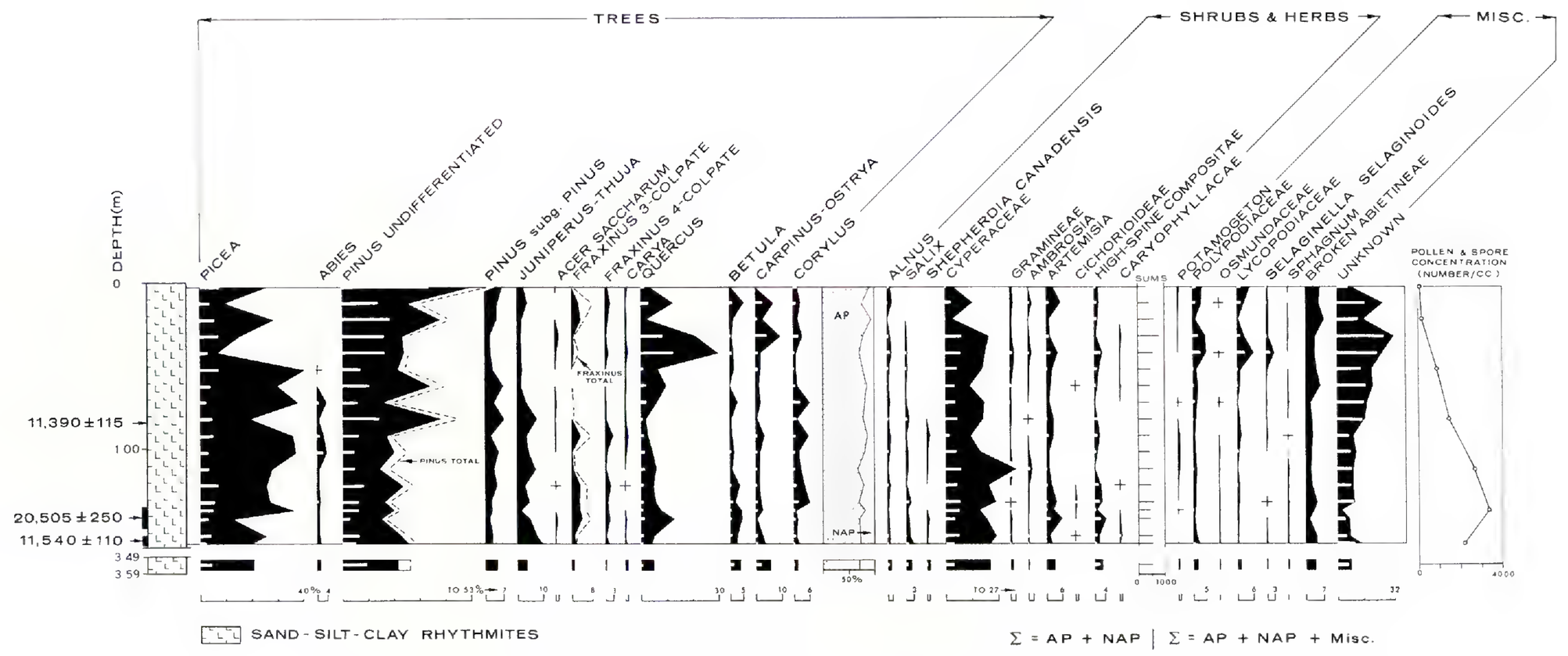

FIGURE 2. Pollen diagram. White bars within silhouettes represent percent deteriorated grains in any category. Most unknown grains too badly preserved to permit more precise identification.

sediments. The three carbon-14 age determinations are next to bars or marks that represent depths from which the analyzed samples were taken. Deteriorated pollen (Cushing, 1964) occurred at all sampled levels, and the white bars within the silhouettes represent percent deteriorated in any category. Percentages of trees, shrubs, and herbs are based on the total number of pollen grains of arboreal and nonarboreal plants at any one level excluding those categories designated miscellaneous. The percentage base for the miscellaneous category is the sum of all items at a given level.

Some pollen types have been subdivided on the basis of morphological characters, as is common in modern pollen analysis. Pollen of *Picea* was not further divided because size and cap thicknesses overlapped too much to allow any subgroups to be distinguished. Of the three curves representing pine pollen, *Pinus* subg. PINUS includes pollen with an observable psilate germinal furrow. No grains with verrucose furrow surfaces (the *Pinus* subg. STROBUS type) were observed. Undifferentiated *Pinus* includes pine pollen in which sculpturing of the distal face could not be seen. Total *Pinus* represents the sum of the two categories, including corroded grains. No deteriorated *Juniperus-Thuja* pollen was recognized. With slight deterioration of this pollen type, the granules are probably destroyed, resulting in a smooth, nondiagnostic, inaperturate body. The *Fraxinus*-total curve is the sum of *Fraxinus* 3- and 4-colpate plus the percentage of deteriorated *Fraxinus*. Deteriorated *Fraxinus* pollen was not divided into 3- and 4-colpate types and is not represented by white bars in the diagram. We interpret 3-colpate *Fraxinus* to be *F. nigra* Marsh.; those with four colpi are other species including *F. americana* L., *F. pennsylvanica* Marsh., and *F. quadrangulata* Michaux.

Pollen and spores in the unknown category were not identifiable for one of the following reasons: deterioration was so great that they were recognized as spores or pollen grains only; preservation was good, but the form was unfamiliar — therefore they could not be assigned to any known family or lower taxon; preservation was good, but the microfossil was folded or obscured by debris, thereby hiding diagnostic features. Unknown microfossils were nearly all badly deteriorated.

Although the sampled sediments probably represent only a few hundred years, percentages of the various recognized pollen and spore types show prominent fluctuations that signal possible ways to subdivide the pollen diagram into zones. However, as will be discussed later, the most important pattern appears related to the sediments being oxidized above 0.75 meter. Below this level *Abies* is uniformly present, *Juniperus-Thuja* is better represented, and increased *Picea* and decreased *Pinus* percentages are apparent. Also in the topmost layers, the percentage of unknown (i.e., mostly deteriorated) microfossils is greatest, and pollen and spore concentration is lowest.

Spectra from unoxidized sediment below 0.75 meter are more reliable indicators of the original unaltered pollen assemblages. About 75 percent of a spectrum below 0.75 meter consists of tree pollen types, with *Picea* and *Pinus* predominating. Most of the pine pollen is of the subg. PINUS

type, which includes *Pinus Banksiana* Lamb. and *P. resinosa* Aiton. Pollen of various deciduous genera of trees or shrubs (*Acer*, *Betula*, *Carpinus* and/or *Ostrya*, *Carya*, *Corylus*, and *Fraxinus*) is present, but percentages of *Acer* and *Carya* are low, and about 10 percent or less each of *Fraxinus* and *Quercus* is present. Pollen from nonarboreal sources (mostly of Cyperaceae) comprises 25–30 percent of the spectra. *Artemisia* and other Compositae are also relatively well represented. Our counts included no pollen of the arctic and alpine herbs that characterize late glacial sediments in southern Quebec (Richard, 1977). The average of four pollen and spore concentration determinations below 0.75 meter is 2435 microfossils per cc.

Macrofossils

Unoxidized megascopic plant fossils occurred mainly between 1.38 and 1.45 meters, and this interval yielded the material upon which the following descriptions are based. Intact specimens were impossible to obtain from the oxidized upper 0.75 meter of sediment, where fossils were too fragile to be freed from the matrix by wet sieving. A continuous record was not obtained below 0.75 meter because organic layers were not always present along the vertical sampling line. Nevertheless, only one macrofossil assemblage appears to be present between 0 meters and the level of the lowest radiocarbon date. The topmost 0.75 meter of sediment, where preservation was poorest, contained several concentrations of limonitic (rust-colored) leaves resting parallel to the bedding planes. Although lacking in morphological detail, all leaf-types found above 0.75 meter are also represented in unoxidized sediments below this level. Similarly, in the nearly 0.5 liter of wet sieve residue that produced wood fragments used for radiocarbon dating the interval 1.52–1.58 meters, no kind of plant fossil was encountered that did not also occur between 1.38 and 1.45 meters.

Species were identified with the aid of an herbarium-vouchered collection of seeds, fruits, and other plant organs that includes all northern species of an identified genus listed in Fernald (1950), as well as all species recognized by Polunin (1940) for the Canadian eastern Arctic and by Scoggan (1950) for the Gaspé Peninsula, Quebec. Because some plants represented in the deposit are characteristic of northwestern North America, particularly western Canada, the listing of Canadian seed plants by Boivin (1966–67) was used as a basis for expanded coverage. In some cases a special effort was made to compare the fossils with species and varieties known exclusively from western America, but the absence of suitable herbarium material and the existence of unsettled taxonomic problems in certain genera made this difficult to do in all cases. Our work on the Columbia Bridge fossils indicates that species of western North America should be considered when identifying late glacial plant fossils from sites in eastern (and probably central) temperate North America.

The brief morphological and taxonomic notes that follow are presented

as partial documentation of the identifications. In some cases more extended discussions are found in APPENDIX B. Ranges are mostly from Fernald (1950) and Hultén (1968) and include only a New World segment of a distribution that may be amphiatlantic or completely or partly circumpolar. Species concepts generally follow Fernald (1950). For infrequent and rare fossils, we give the number of specimens recovered, but these figures are only a general indication of abundance. They are based on the number of intact fossils recovered from about 1.5 liters of wet sieve residue, which was comprised mostly of degraded and unidentifiable plant material. The number of recovered intact fossils probably does not accurately reflect vegetation composition.

Equisetum sp. Three aerial stem fragments (stomata visible), including nodes with whorled leaves, chartaceous leaf tips worn away; one rhizome fragment. In size the specimens agree best with *E. pratense* Ehrh., *E. scirpoides* Michaux, and *E. variegatum* Schleicher, all of which are northern and transcontinental in distribution, although small specimens of other species, such as *E. arvense* L., are also similar. Unfortunately, cortical tissues and the system of internal canals, which provide characters of taxonomic value, are absent in the specimens.

Selaginella selaginoides (L.) Link. Two megaspores; also microspores (see FIGURE 2). Megaspores of *S. selaginoides* are finely punctate; those of *S. apoda* (L.) Fern. and *S. rupestris* (L.) Spring are reticulate. A species of calcareous habitats, and in North America the most northern of the three species, *S. selaginoides* occurs from Greenland and Labrador to Alaska, and, in the East, south to northern Maine and the upper Great Lakes region.

Woodsia ilvensis (L.) R. Br. A pinna, margins revolute, with dorsal uniseriate trichomes. In other northern species of *Woodsia*, leaf margins are plane to weakly revolute, or fronds are glabrous or have conspicuous glandular trichomes. Scales, which arise from the underside of fronds of *W. ilvensis*, were not seen in the fossil. The species occurs in exposed, rocky habitats from the eastern Arctic, south to Pennsylvania and North Carolina (uplands only), and west to Alaska and British Columbia. FIGURE 3.

Picea sp. Ten well-preserved needles and one cone scale (5 mm. long, 4 mm. wide), with the wings of both seeds visible. The scale is wedge shaped, and its dorsal surface is divided into a distal smooth portion

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FIGURES 3–13. Plant macrofossils from Columbia Bridge site. 3, *Woodsia ilvensis*: pinna, lower surface. 4–8, *Juniperus communis*: 4, 5, branch tips; 6, isolated needles; 7, microsporangiate cone; 8, fleshy, ovulate cone. 9, 10, *Salix vestita*, two leaves: 9, upper surfaces; 10, lower surfaces. 11, 12, *Populus balsamifera*: 11, leaf fragment, glands at both sides of petiole apex; 12, capsule, note basal disc. 13, *Oxyria digyna*: fruit, outer parts of wing absent. Scale lines = 1 mm.

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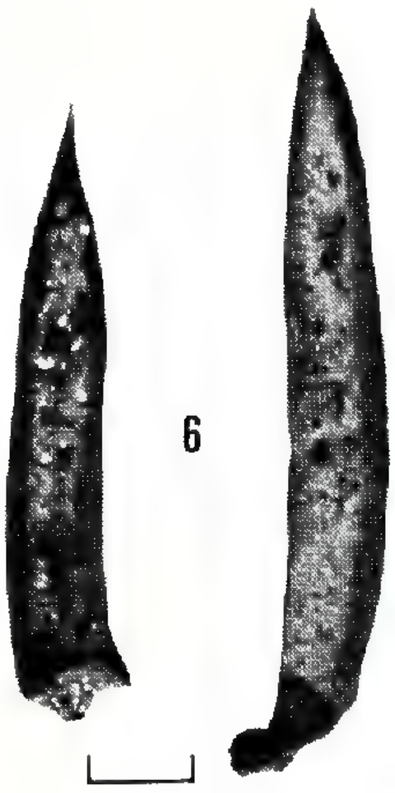
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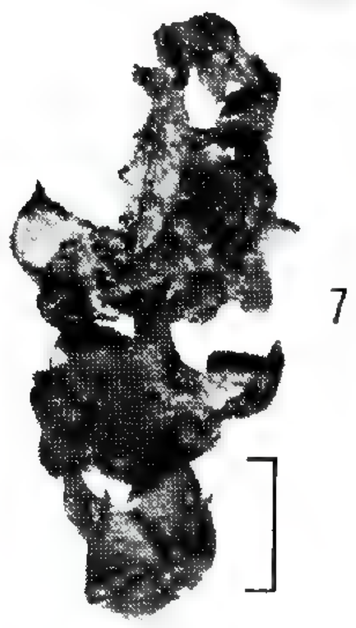
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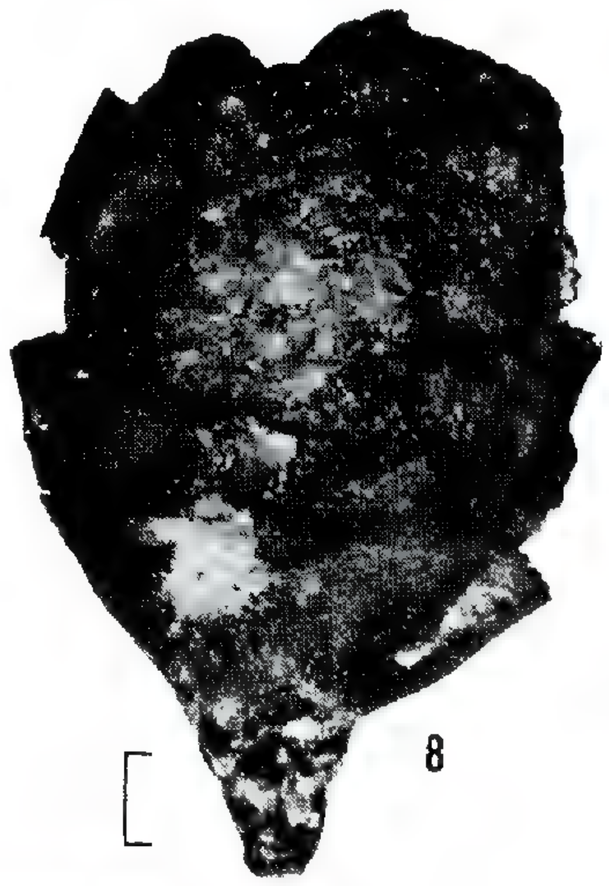
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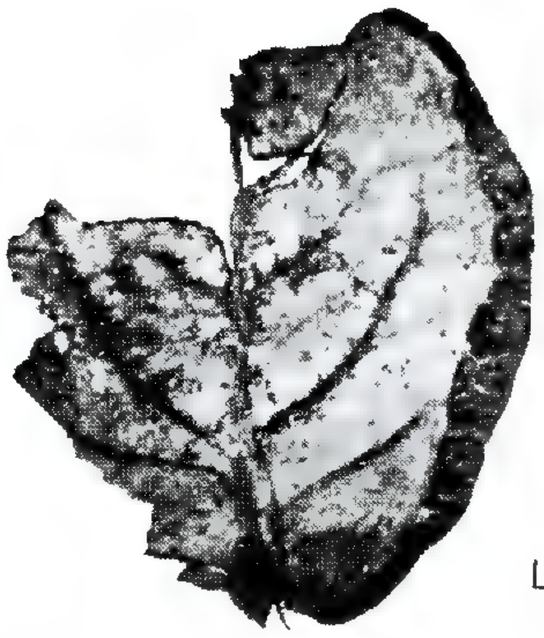
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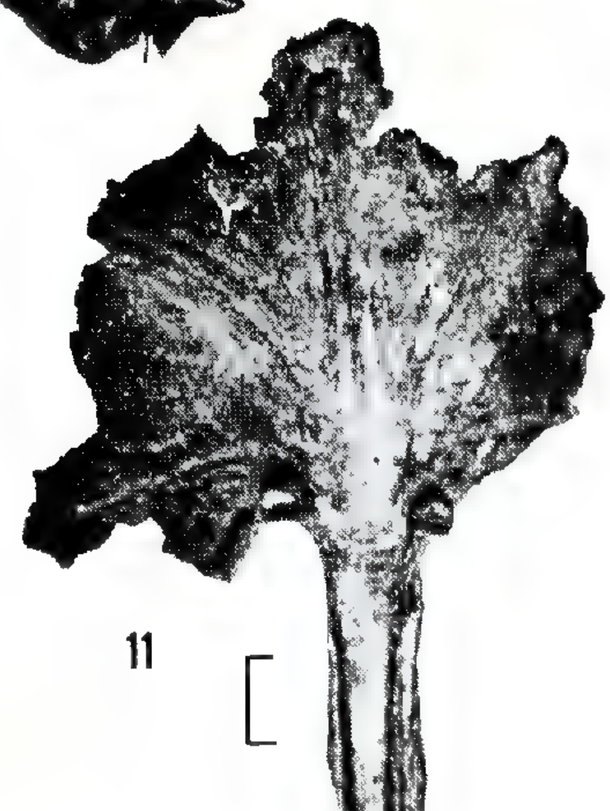
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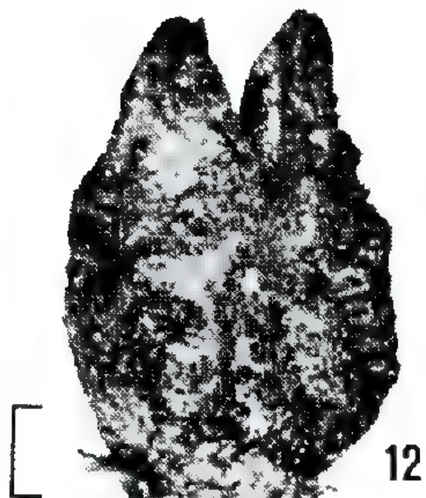
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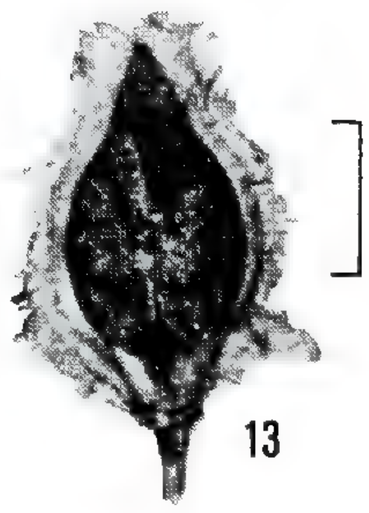
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(umbo) and a proximal area of different texture. These features rule out *Abies*, *Larix*, *Pinus*, and *Thuja*. Macrofossils of spruce are poorly represented in the deposit, but at least some reproducing individuals grew near the site.

Juniperus communis L. Twenty-one isolated needles, seventeen branch tips with attached needles, two fleshy ovulate cones, two seeds, and one microsporangiate cone. Mean needle length (n = 21) is 6.1 mm.; ovulate cones measured 8 and 5 mm. wide. Of the several varieties of *J. communis* recognized by Fernald (1950), the fossil needles are too short for vars. *communis* and *depressa* Pursh, while the ovulate cones are too small for var. *megistocarpa* Fern. The fossils best match var. *saxatilis* Pallas, which grows in exposed places from Greenland to Alaska, and in the East as far south as the mountains of northern Maine. FIGURES 4–8.

Potamogeton filiformis Pers. Twenty-seven endocarps, some with portions of the exocarp still adherent, indicating the absence of a lengthy period of predepositional transport. Identification of pondweed fruits is facilitated by the works of Aalto (1970), Jessen (1955), and Martin (1951). Diagnostic fruit characters of *P. filiformis* include size (ca. 2.5 mm. long, 2 mm. wide) and a rounded lid (crest present in fruits with exocarps intact) that ends well below the style, which is more or less centrally placed as opposed to being nearer the ventral side as in the similar *P. vaginatus* Turcz. Aalto (1970) indicated that the base of the lid does not taper in *P. filiformis*, while it is V shaped in *P. vaginatus*, but this distinction does not appear to hold for the North American material that we studied of these species. Based in part on size measurements given by Martin (1951), which are in general larger than those of Aalto (1970), we have identified the specimens as *P. filiformis*, a species of calcareous, sometimes brackish waters from Greenland to Alaska and southward sporadically to northern New England, Minnesota, and Nevada. FIGURES 14, 15.

Potamogeton pusillus L. One endocarp. Fruits of this pondweed are small (2 mm. long, 1.5 mm. wide) and have an S-shaped ventral margin and a convex lid that extends to the style base. The species occurs in cal-

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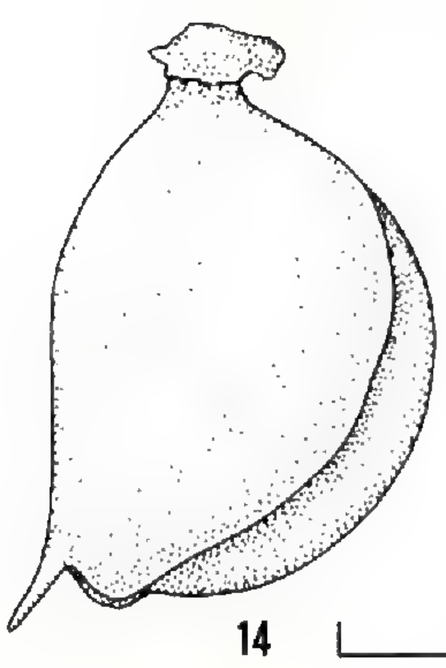
FIGURES 14–31. Plant macrofossils from Columbia Bridge site. 14, 15, *Potamogeton filiformis*: 14, lateral view of endocarp, stigma at top; 15, endocarp in longitudinal section showing embryo cavity and lid apex, which ends well below style. 16–19, *Carex bipartita*: 16, fossil, ventral side of perigynium (achene in place); 17, fruit from herbarium specimen, same view; 18, same fossil, dorsal side of perigynium; 19, fruit from herbarium specimen, same view (17, 19, from Canada, Newfoundland, hills east of Little Quirpon Harbour, *Fernald & Gilbert 27622*, 8 Aug. 1925 (GH)). 20, *Carex aquatilis*: perigynium, achene in place. 21, *Betula* cf. *glandulosa*: winged fruit. 22, *Polygonum ramosissimum* cf. var. *prolificum*: achene with fragment of calyx adherent at base. 23, *Arenaria* cf. *dawsonensis*: seed. 24, 25, *Ranunculus Cymbalaria*: two achenes. 26, *Saxifraga aizoides*, seeds: right, fossil; left, from herbarium specimen (Canada, Québec, Gaspé Peninsula, bluffs and slopes, Bonaventure River, *Collins et al. 5222*, 5, 6,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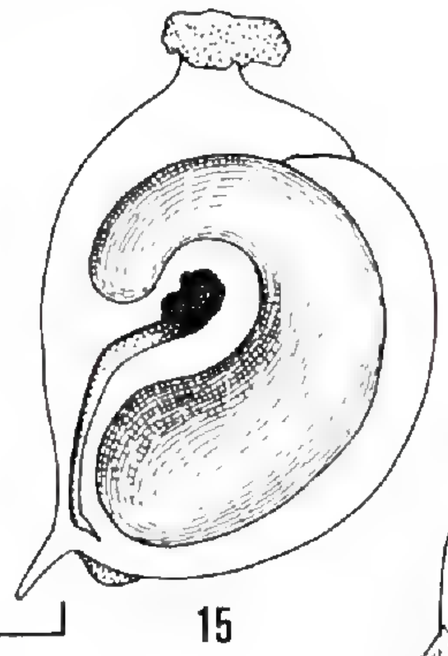
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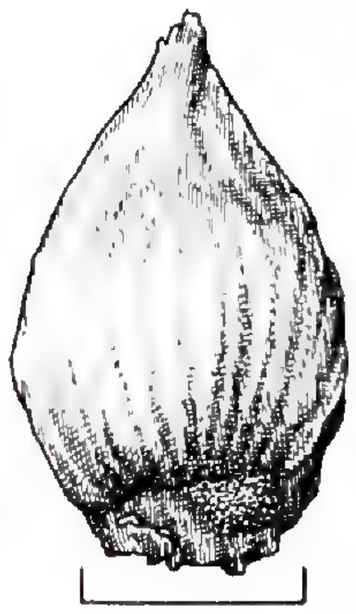
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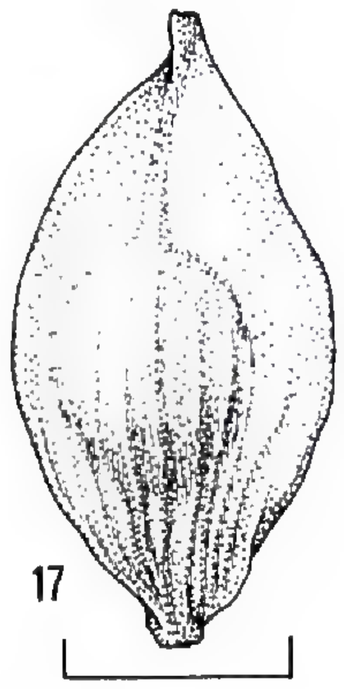
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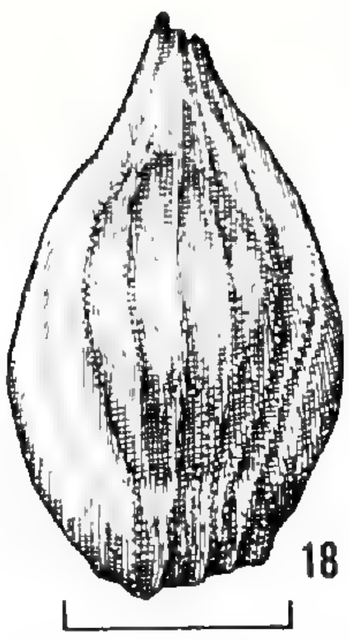
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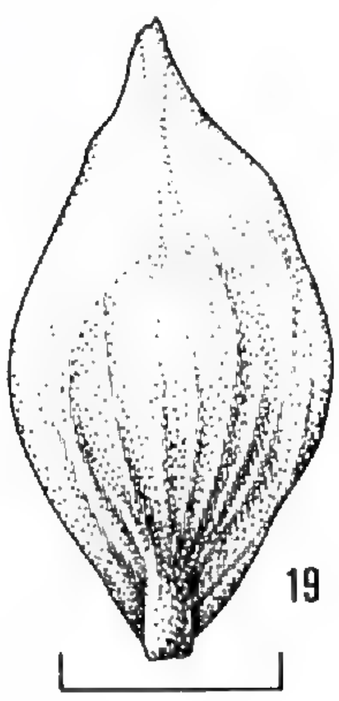
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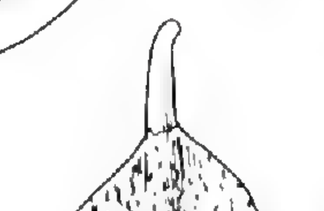
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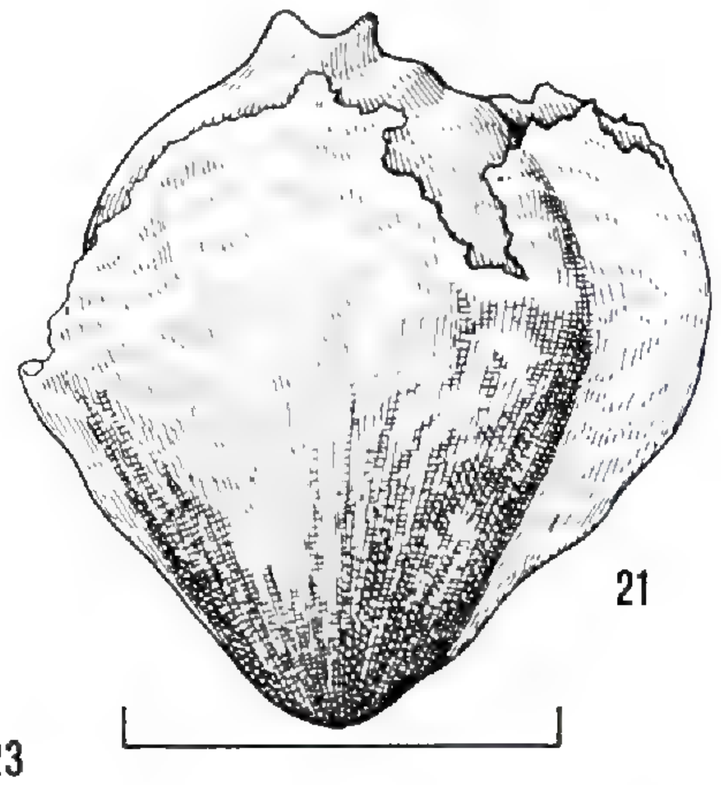
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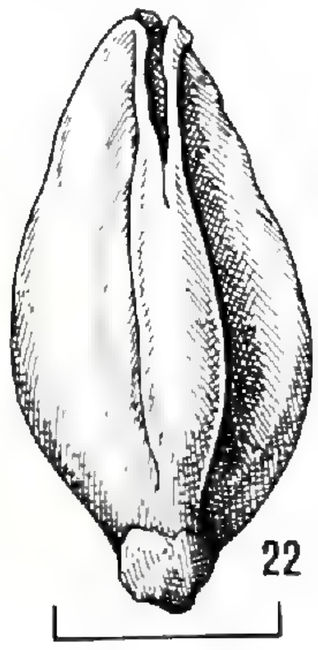
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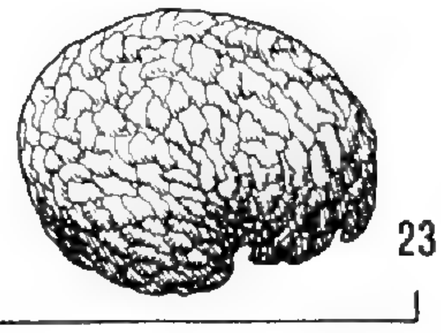
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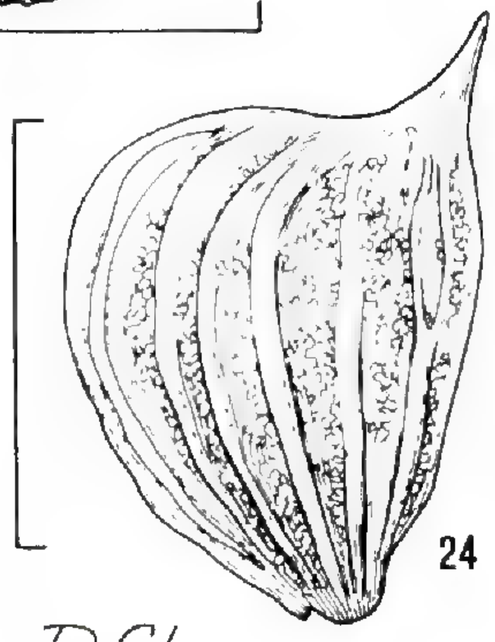
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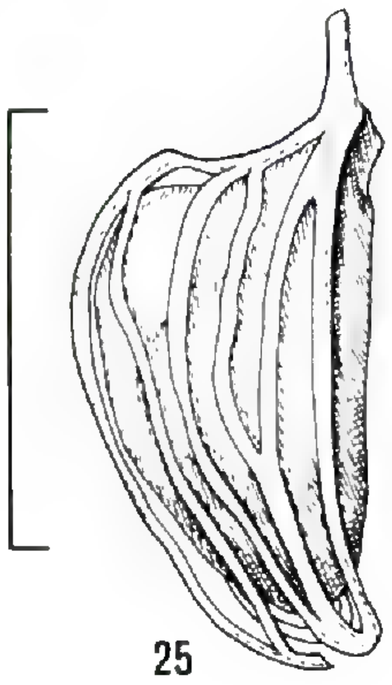
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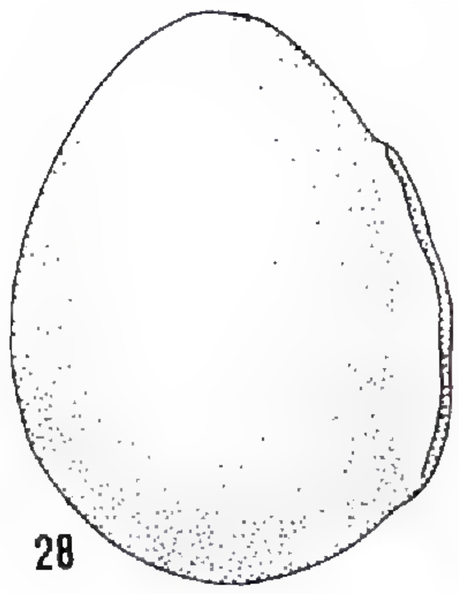
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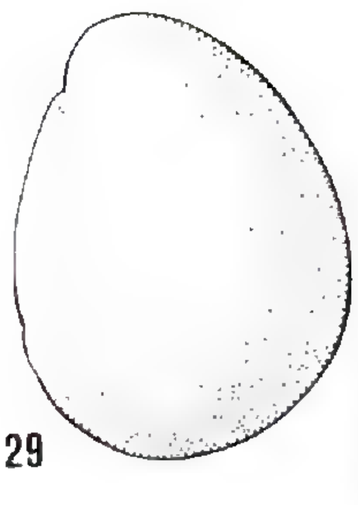
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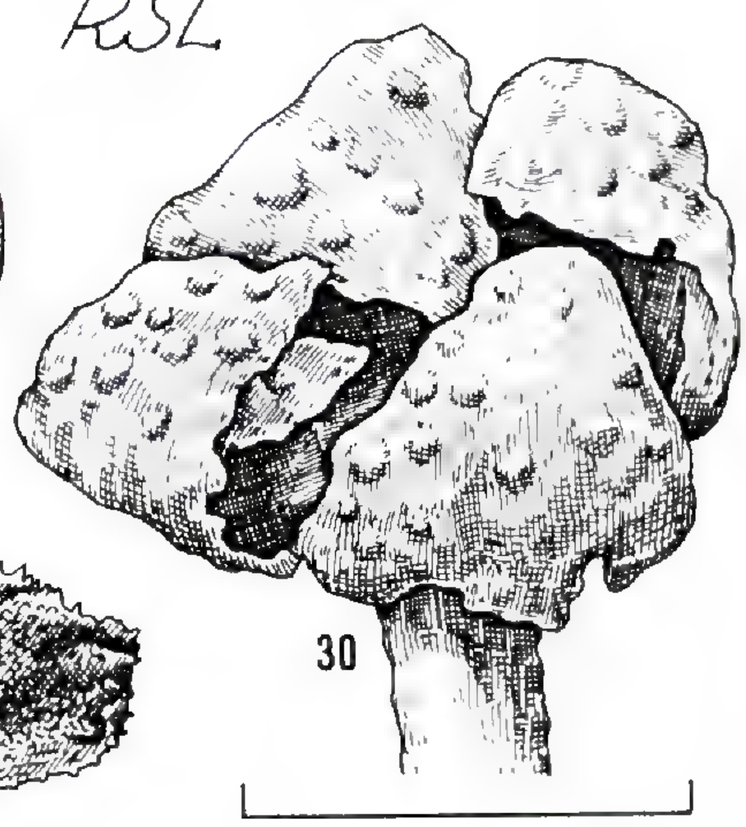
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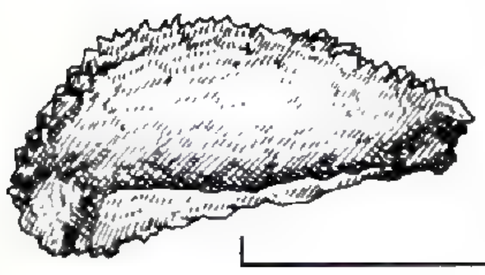
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& 8 Aug. 1904 (GH)). *27*, *Parnassia* cf. *Kotzebuei*: seed, cellular testa partly broken away. *28*, *Sibbaldia procumbens*: achene. *29*, *Potentilla* sp.: achene. *30*, *Shepherdia canadensis*: staminate flower. *31*, unknown composite: achene. Scale lines = 1 mm.

careous waters from Gaspé County, Quebec, to northern Alberta, and in eastern North America south to Louisiana and Texas.

Both *P. filiformis* and *P. pusillus* have narrow leaves (less than 1 mm. and to 3 mm. wide, respectively). Much wider *Potamogeton* leaves were reported by Hollick (1931) from the Columbia Bridge beds. These are similar to leaves (ca. 1 cm. wide) we also observed at many places in the lower part of the section. Their specific identity is unknown.

Carex bipartita Bellardi ex All. One perigynium, achene in place. Although the base and apex of the perigynium are imperfectly preserved, the fruit belongs to sect. HELEONASTES Kunth because of its rounded, wingless margins, short beak, and lenticular achene. The fossil compares well in size and shape with *C. brunnescens* (Pers.) Poiret but lacks the serrulate beak of that species. In all important features it matches fruits of *C. bipartita*, a sedge of subarctic and arctic regions from Greenland to Alaska, south to the mountains of the Gaspé Peninsula, Quebec, in the East, and to Colorado and Utah in the West (Hermann, 1970). It is a calcicole on the Gaspé Peninsula (Scoggan, 1950). In the Arctic the species grows on moist to wet sand and turfy places near streams and lakes or on hillsides (Polunin, 1940; Porsild, 1964). FIGURES 16–19.

Carex aquatilis Wahlenb. Five perigynia with achenes. The perigynia are biconvex, and the achenes, which are visible with transmitted light, lack a lateral constriction and do not fill the perigynium apex. These are features of *Carex* sect. ACUTAE, and, of possible species in this section, the fossils agree best with the variable *C. aquatilis*. Linear groups of red-pigmented cells are present in a few of the perigynia. Similar puncticulae are evident in some herbarium specimens of the species. A sedge of wet sites (shallow pools, pond margins, river banks, and wet meadows), the species ranges from Greenland to Alaska, south to Quebec, northern Michigan, Arizona, and California (Hermann, 1970). FIGURE 20.

Sedge achenes are the most abundant seed- and fruit-type in the deposit. Species other than those listed above are represented as judged from the different sizes and shapes of both lenticular and trigonous types among the 85 sedge achenes recovered from the sieve residues. No attempt has been made to identify these.

Salix vestita Pursh. Seventeen leaf fragments, five of which include petioles. The leaves are obovate or elliptic and have rugose upper surfaces, pubescent undersides, and revolute margins. Hollick (1931) listed *S. reticulata* L. as a member of the Columbia Bridge flora, but to judge from published photographs of fossils so named, his specimens could be *S. vestita*. In our carbonized and fragmented but otherwise unaltered fossils, small resinous glands occur on the petiole margins and at the edges of the leaves near the petiole. Such glands do not occur in *S. reticulata* but appear diagnostic for *S. vestita*. An ascending shrub of calcareous soils in boreal and subarctic areas from Newfoundland and Labrador to northern and eastern Quebec, *S. vestita* also occurs disjunctively westward in north-

western Ontario and adjacent Manitoba, in the mountains along the border between southern Alberta and British Columbia, and at a few places in the northwestern United States (FIGURE 69). George W. Argus, a specialist on American willows, has confirmed the identification. FIGURES 9, 10.

Salix cf.[2] **Uva-ursi** Pursh. Fragmentary leaves, one a complete leaf base with veins that run parallel to the margin (which is entire, as is usual for leaves borne lower on shoots of this willow; G. Argus, *in litt.*), and three fragments with marginal teeth that are too widely spaced to compare well with those of *S. herbacea* L. Leaves of *S. Uva-ursi* vary from elliptic to obovate, with the apex acute to obtuse, the base attenuate, and the margins dentate, crenulate, or subentire to entire. Leaves of *S. herbacea* are widely elliptic, with the apex usually obtuse or retuse and the base more or less cordate. Capsules recovered from the deposit (n = 37) are glabrous, have tapered beaks of moderate length, and also match those of *S. Uva-ursi* in size. *Salix Uva-ursi* is a willow of the eastern North American Arctic (Greenland to the east coast of Hudson Bay) that occurs southward to the alpine areas of Quebec and northern New England, and New York.

Salix cf. **argyrocarpa** Andersson or **S.** cf. **pellita** Andersson. Fifteen leaves and fragments, none over 1 cm. in length, and five fragments with petioles and part of the leaf blade; margins entire in all specimens. The fossil leaves are narrowly elliptic, attenuate, and strongly revolute at the base, and have a deep groove on the adaxial face of the petiole. Young leaves of *S. pellita* are similar in shape to mature leaves of *S. argyrocarpa*, although fully developed leaves of the former can be 10 cm. or more in length. Leaves of both species may have entire or crenulate margins. While the recovered fragments are all small, complete limonitic leaves of similar shape but larger size (to 4 cm.) were found in the upper, oxidized part of the deposit. These match herbarium material of *S. pellita*, but a positive identification is not possible. *Salyx argyrocarpa*, a shrub of moist alpine or subalpine meadows, occurs from Labrador south to northern New Hampshire; *S. pellita*, which has a similar range (southern Labrador south to northern New England and Michigan), usually does not grow at higher elevations.

Both species were listed by Hollick (1931), but neither the limonitic leaves available to him nor the newly collected carbonized fragments, in our opinion, present sufficient characters for unequivocal identification.

Populus balsamifera L. Abundant material including limonitic leaves, a carbonized leaf base and petiole, bud scales, six capsules or capsule valves, and seeds of a *Populus*, probably of *P. balsamifera*. Hollick (1931) identified limonitic leaf fossils of similar appearance as *P. balsamifera* and *Celtis occidentalis*. However, we can find no consistent differences between

[2] The designation "cf." means that the fossil compares well with recently collected material of the species, but for some reason a conclusive identification cannot be made.

his illustrations of fossils given these names and suggest that material referred to *Celtis* is, in fact, *P. balsamifera*. No fossils of *Celtis* were found by us, and, in their absence, as well as for ecological reasons, it seems justifiable to drop from the flora *C. occidentalis*, a species now rarely found north of southern New England.

Capsules of *Populus* have a basal disc (FIGURE 12), while those of most willows (species of sect. RETICULATAE Fries excepted) lack this character. Capsules of *P. balsamifera* are large (to 8 mm. long) and strongly rugose; those of *P. grandidentata* Michaux and *P. tremuloides* Michaux are smaller and less rugose; those of *P. deltoides* are larger and do not taper to a prominent beak. The fossil seeds are narrowly oblong (2 mm. long, 1 mm. wide) and have a short apical point and an obtuse base. The fossil bud scales are mostly long (to 1.5 cm.), black, and resinous and compare well with bud scales of *P. balsamifera* and *P. deltoides*. The leaf base illustrated in FIGURE 11 is probably of *P. balsamifera*, although similar glands occur near the petiole apex in other poplars. (They are especially prominent in leaves of *P. deltoides* but are not present on all leaves of *P. balsamifera* and are inconspicuous in herbarium specimens of *P. grandidentata* and *P. tremuloides*.) Glands resembling those illustrated are found at the petiole apex in *Viburnum edule* (Michaux) Raf. and *V. trilobum* Marsh., but in *Viburnum* the glands are stalked and usually somewhat foliar.

Except in northern United States and southern Canada, where the species occurs in the coniferous-hardwood zone, the range of *Populus balsamifera* mostly coincides with the transcontinental boreal forest region. In the East it extends southward to northern New England and New York (sporadically beyond), and to Michigan, northern Wisconsin, and Minnesota. It is a pioneer along streams and rivers and in other disturbed situations. FIGURES 11, 12.

Betula cf. **glandulosa** Michaux. One fruit, wings poorly preserved. Birch fruits differ in size, width and shape of the wings, and size and shape of the central seed. Based on its size (2 × 2 mm.), its narrow wings, which are broader toward the apex, and its wedge-shaped seed base, the fossil is probably *B. glandulosa*. Fruits of *B. pumila* are sometimes slightly larger (3 mm. wide, 2 mm. high) and generally have somewhat broader wings; those of *B. nana*, which Hultén (1968) maps as being transcontinental across the Canadian Low Arctic, are the same size as those of *B. glandulosa* and in at least some specimens have wings about half as broad as the central body. Mature carpellate cone bracts of the three species are also usually similar in size and shape, and the resinous hump on the back of bracts of *B. glandulosa* (Hultén, 1968) may or may not persist during fossilization. Examination of collections in the combined herbaria of the Arnold Arboretum and Gray Herbarium indicates that fruit and carpellate cone bract characters may not be diagnostic for *B. glandulosa*, *B. nana*, and *B. pumila*. As interpreted by Hultén (1968), *B. glandulosa* occurs across boreal North America (but extending farther south than *B. nana*) from Greenland to Alaska, and in the East southward to alpine areas of

Quebec, Maine, New Hampshire, and New York. *Betula pumila* is a plant of bogs and wooded swamps from Newfoundland to British Columbia, and south sporadically to the northern United States. FIGURE 21.

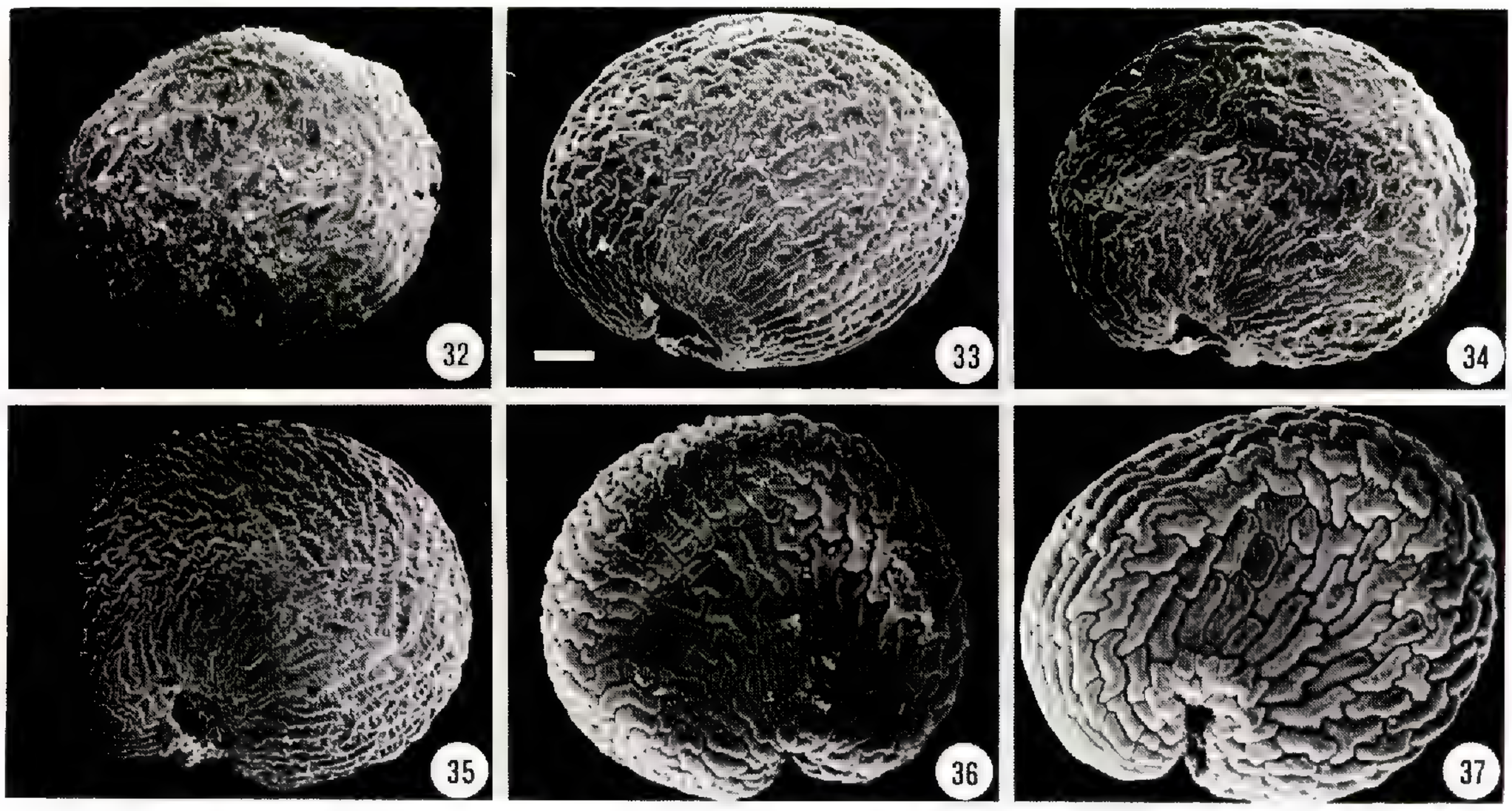
Oxyria digyna (L.) Hill. One fruit, peripheral parts of wing absent, achene lenticular. An arctic-alpine species that is known in eastern North America as far south as the mountains of the Gaspé Peninsula and northern New Hampshire. FIGURE 13.

Polygonum ramosissimum Michaux cf. var. **prolificum** Small (*P. prolificum* (Small) B. Robinson). Four achenes, calyx base persisting in fossils. Identification is based on the triangular (and 3-angled) shape of the achenes, whose concave sides lack pits or punctae. The fossils are similar in shape to achenes of *P. buxiforme* Small (*P. aviculare* var. *littorale* (Link) W. D. J. Koch; see Mitchell & Dean, 1978) but differ from fruits of this species in lacking punctae. The identity of the fossil material was suggested by R. S. Mitchell. *Polygonum ramosissimum* is a plant of sandy and light soils along shores and in disturbed habitats (roadsides) in temperate areas of North America (New England and southwestern Quebec to Washington, and south to Pennsylvania and Texas); var. *prolificum* has a similar range. FIGURE 22.

Arenaria cf. **dawsonensis** Britton. One seed. The identity of the fossil is uncertain because of somewhat poor preservation and sediment-obscured intercellular areas, which do not allow a satisfactory match with herbarium reference specimens. *Arenaria dawsonensis* is distributed westward from southern Labrador and Newfoundland to Yukon and Alberta, and in the East as far south as eastern Quebec. It is a plant of calcareous ledges and gravel. See APPENDIX B. FIGURES 23, 32, 33.

Silene acaulis var. **exscapa** (All.) DC. One seed, cells of seed coat black and bulging, anticlinal walls of seed coat cells strongly undulate. Although the testa is somewhat abraded and obscured by small sediment particles, the fossil fits within the variation observed in seed samples of New World populations of *S. acaulis* (FIGURES 39–41). The distorted part of the seed coat near the hilum (FIGURE 38) is where the radicle emerges at germination; thus the fossil may be of a germinated seed. *Silene acaulis* var. *exscapa* occurs across subarctic and arctic America, and in the East it is found south to alpine areas of Quebec and New Hampshire. FIGURES 38–41.

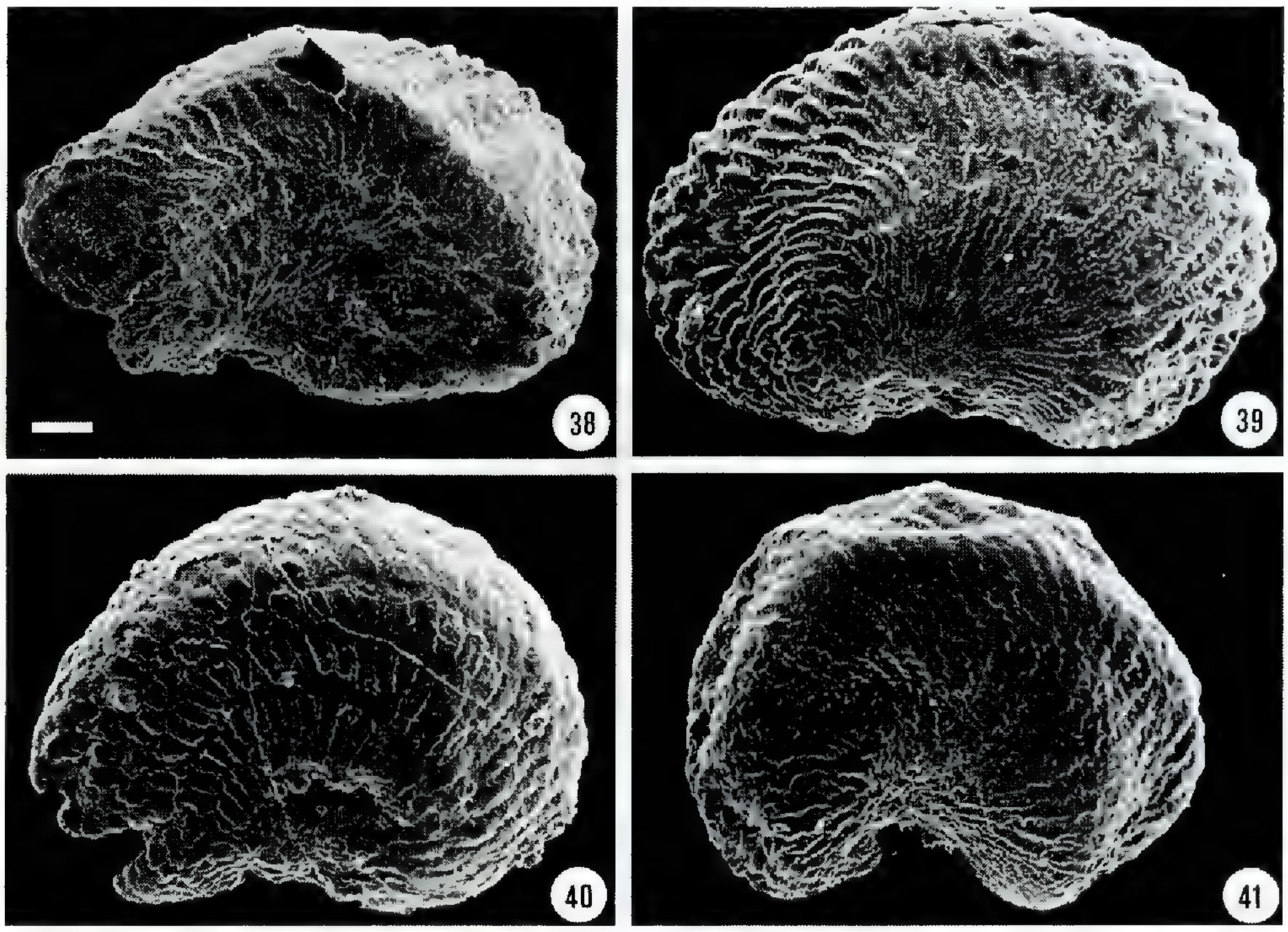
Ranunculus Cymbalaria Pursh. Two achenes. Fruits of species of *Ranunculus* are smooth, pitted, punctate, or longitudinally (*R. Cymbalaria* only) or transversely ribbed. Longitudinally ribbed fruits of species of *Thalictrum* (e.g., *T. alpinum* L.) differ from those of *R. Cymbalaria* in shape and in the more centrally placed style. *Ranunculus Cymbalaria* is distributed across northern North America from southern Greenland to Alaska, and south to New Jersey and Arkansas in the East. FIGURES 24, 25.



FIGURES 32–37. Scanning electron micrographs, seeds of species of *Arenaria*: 32, *A.* cf. *dawsonensis*, fossil seed, sediment particles visible on surface; 33, *A. dawsonensis* (Canada, Newfoundland, Mt. Musgrove and Humber Mouth, *Fernald & Wiegand 3355*, 18 July 1910 (GH)); 34, *A. uliginosa* Schleicher in Lam. & DC. (*A. stricta* Michaux *s. l.*, *fide* Boivin, 1966–67) (Canada, N.W.T., Smith Arm, Great Bear Lake, *Porsild & Porsild 5077*, 16–21 July 1928 (GH)); 35, *A. Rossii* (Canada, N.W.T., South Bay, Southampton Island, *Polunin 2282*, 22 Aug. 1936 (GH)); 36, *A. patula* (U.S.A., Kentucky, Mundy's Landing, *Wharton 8914* 25 May 1955 (GH)); 37, *A. stricta* (U.S.A., New York, Essex County, Lower Jay, *House 10283*, 11 July 1924 (GH)). White bar = 100 μm.

Draba sp. One fruit, badly preserved and containing no seeds (small, black ascocarps visible on capsule surface), but agreeing in size and shape with several northeastern North American species of this genus. Nineteen native species of *Draba* are listed by Fernald (1950) for the *Gray's Manual* area, eleven species are credited to the Gaspé Peninsula, Quebec (Scoggan, 1950), and eight are given by Polunin (1940) for the Canadian eastern Arctic. The genus is especially rich in calcicoles. FIGURE 42.

Saxifraga aizoides L. One seed, spines visible, but cell walls of testa obscured by sediment particles. Seeds of northeastern North American *Saxifraga* species, excluding the rarely fruiting *S. cernua* L. and the geographically isolated *S. gaspensis* Fern. and *S. Geum* L. (which were not studied), have variously ornamented testas (see APPENDIX B). However, only in fully mature seeds of *S. aizoides* do cells of the testa extend outward as long, sharply defined spines. In seed shape and spine arrangement the fossil seed agrees closely with modern reference specimens, and the only difference would seem to be a greater number of spines in the fossil. In North America *S. aizoides* ranges from southern Greenland to Newfoundland, and west to Yukon and eastern British Columbia; it is principally a plant of subarctic and arctic latitudes (although absent from much of the Canadian Arctic Archipelago). In the East *S. aizoides* occurs



FIGURES 38–41. Scanning electron micrographs, seeds of *Silene acaulis* var. *exscapa*: 38, fossil seed from Columbia Bridge site, distorted area at lower left is where radicle breaks through seed coat at germination (see FIGURE 40); 39, seed from herbarium specimen (Canada, Quebéc, Wakeham Bay, Hudson Strait, *Malte 126956*, 24 July 1933 (GH)); 40, seed recovered from soil adhering to specimen, note ruptured seed coat and fungal hyphae (same collection as in Figure 39); 41, seed from herbarium specimen, possibly less mature than that in FIGURE 39 (Canada, Newfoundland, Bay of Islands region, *Fernald & Wiegand 3398*, 24 July 1910 (GH)). White bar = 100 μm.

southward at a few widely scattered places in New England to eastern and western New York. These outlying stations are mostly faces and ledges of wet, calcareous cliffs. FIGURES 26, 82–85.

Parnassia cf. **Kotzebuei** Cham. Two seeds, part of the loose, cellular seed coat broken away. In eastern North America, excluding two species of *Parnassia* that extend north only to Virginia, four species are northern (boreal forest or subarctic) in distribution. Seeds of one of these, *P. parviflora* DC., have less distinctly reticulate seed coats and are smaller than seeds of the other species. Seeds of *P. glauca* Raf. and *P. palustris* var. *neogaea* Fern. are the same size as those of *P. Kotzebuei*, but the cellular testa is less pronounced and shiny. We consider the identification of the fossils probable, but not positive, because cells of the testa may have been modified during fossilization. *Parnassia Kotzebuei* exhibits an interrupted range across northern continental North America (southern and western Greenland, northwestern Newfoundland, Gaspé, northern Quebec, Labrador, and from the northwest coast of Hudson Bay to Alaska). FIGURE 27.

Sibbaldia procumbens L. Two achenes, which differ from those of *Potentilla* in having apices central and obtusely rounded (cf. FIGURES 28,

29). An arctic-alpine species of disjunct distribution in North America; in the East occurring from southern Greenland to Hudson Bay (and at scattered stations to the west) and southward in the mountains of northwestern Newfoundland, Gaspé, and New Hampshire; in the West from Alaska to California, Utah, and Colorado. FIGURE 28.

Potentilla spp. Seven achenes of different size classes, possibly representing three species; all specimens have smooth walls. The fossils compare favorably in size and shape with achenes of the following northern species of diverse habitats: *P. gracilis* Douglas, *P. hyparctica* Malte, *P. nivea* L., *P. pulchella* R. Br., *P. Robbinsiana* Oakes (endemic to White Mountains, New Hampshire), *P. rubricaulis* Lehm., and *P. usticapensis* Fern. See also APPENDIX B. FIGURE 29.

Dryas integrifolia M. Vahl. Numerous isolated leaves and a few leafy plant apices. The fossil leaves are variable in size (3 mm.–1 cm. long) and shape, with margins revolute, entire or sometimes crenulate-dentate. Hollick (1931) identified questioned leaf material of *Kalmia polifolia* Wangenh., *Loiseleuria procumbens* (L.) Desv., and *Vaccinium macrocarpon* Aiton from the Columbia Bridge beds. Study of Hollick's illustrations, in addition to our examination of newly collected limonitic fossils similar to those illustrated by him, suggests that specimens so designated are actually *Dryas integrifolia*. Fossil leaves of *D. integrifolia* are known from several late glacial deposits in Minnesota and at places eastward to Massachusetts (Miller & Benninghoff, 1969), as well as from older late Wisconsinan deposits in this same general region. The species is widespread in arctic North America, where it is a pioneer on raw soil along rivers, cliffs and talus, and beach ridges, particularly on calcareous soils or rock. In eastern North America it occurs southward sporadically to western Newfoundland, Gaspé and Lake Mistassini, Quebec, and southeastern New Brunswick (see map in Miller & Benninghoff, 1969). FIGURES 43–49.

Dryas Drummondii Richardson. Abundant leaves; leaf material of this and the preceding species are the most abundant recognizable plant fossils in the deposit. The leaves vary in shape from elliptic to obovate, with bases cuneate in most (a diagnostic character, according to Porsild, 1947) and margins dentate to the apex. A few of the fossil leaves are white-tomentose beneath. Fossils in FIGURES 52–60 were selected to illustrate variation, but leaves of such diverse form can nevertheless be found on herbarium specimens consisting of one or a few plants. *Dryas Drummondii* exhibits an interrupted western–eastern North American distribution (in the East known only from southwestern Newfoundland, Anticosti Island, and the Gaspé Peninsula), with isolated stations along the north shore of Lake Superior (FIGURE 70). It is a plant of calcareous cliffs, talus, and river gravels. FIGURES 52–60.

Achenes (plumose styles absent) and receptacles with part of the scape attached were also found. It appears impossible to assign such material to either of the two species. FIGURES 50, 51.

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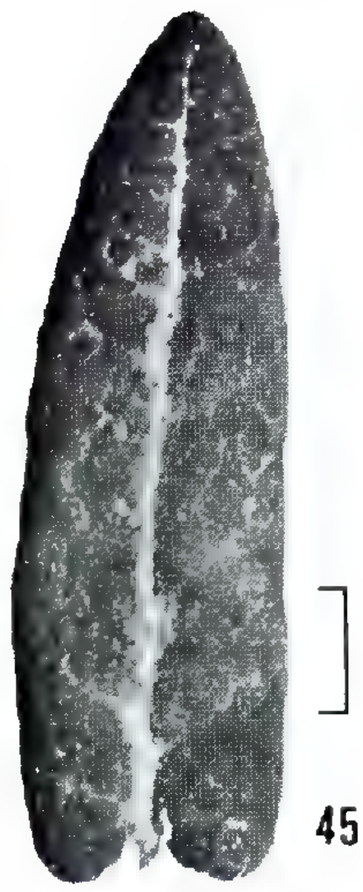

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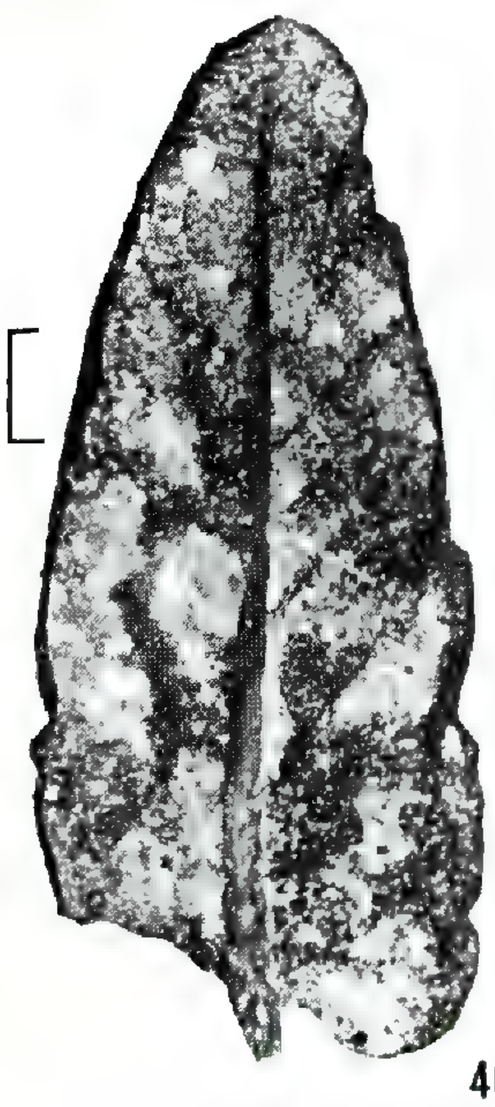

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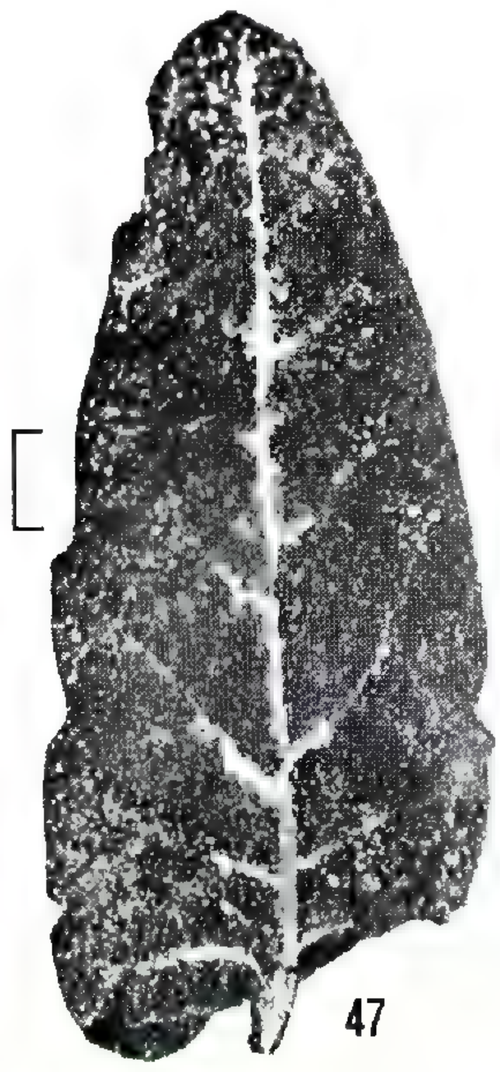

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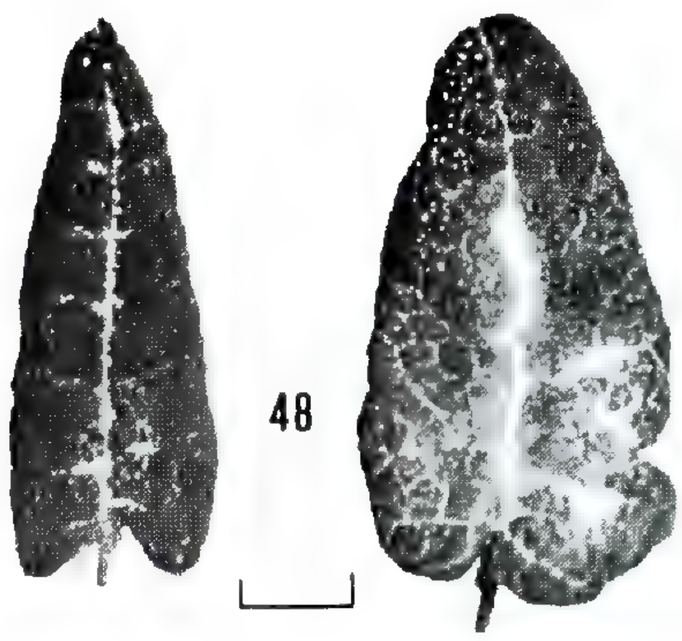

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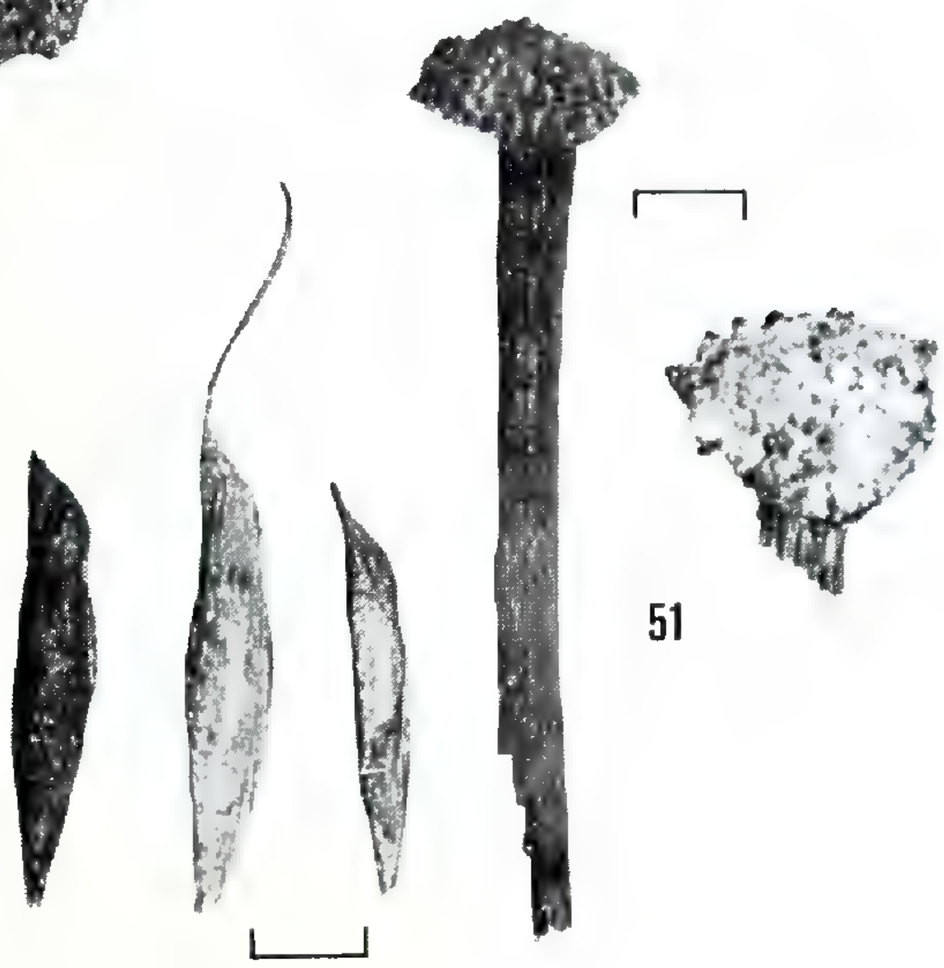

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FIGURES 42–51. Plant macrofossils from Columbia Bridge site. 42, *Draba* sp.: capsule. 43–49, *Dryas integrifolia*: 43, portion of plant with two leaves; 44, leaf, lower surface; 45, same leaf, upper surface; 46, leaf, lower surface; 47, same leaf, upper surface; 48, two leaves, upper surfaces; 49, four leaves, (from left) lower, upper, lower, and upper surfaces. 50, *Dryas* sp.: three achenes. 51, *Dryas* sp.: two receptacles, scapes partly preserved. Scale lines = 1 mm.

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FIGURES 52–60. Plant macrofossils from Columbia Bridge site. *Dryas Drummondii*: 52, leaf, upper surface; 53, same leaf, lower surface; 54, leaf, upper surface; 55, same leaf, lower surface; 56, leaf, upper surface; 57, same leaf, lower surface; 58–60, three other leaves, upper surfaces. Scale lines = 1 mm.

Geum sp. Two receptacles, achenes immature, styles recurved, petals absent, calyx weakly campanulate; further identification not possible because of incomplete preservation. Fernald (1950) lists eight native species for temperate eastern North America. They are plants of dry to moist mineral soils, sometimes wet peats, usually in sparse woods or thickets. *Geum macrophyllum* Willd. and *G. rivale* L. extend northward to southern Labrador.

Elaeagnus commutata Bernh. ex Rydb. One ellipsoid body representing the hardened and eight-ridged inner wall of the calyx tube; four immature fruits with the calyx tube more or less enlarged and fleshy and a portion of the perianth and style persisting, peltate scales visible as punctae. A shrub of dry calcareous slopes, *E. commutata* exhibits an interrupted transcontinental range (FIGURE 70), with eastern stations limited to the Gaspé Peninsula and westward along the St. Lawrence River valley; the western segment of its range extends from the James Bay region to central Alaska, south to northern Utah. FIGURES 61–63.

Shepherdia canadensis (L.) Nutt. Two seeds, one staminate flower, and four twigs with opposite leaf scars or terminal, appressed, paired leaves; peltate scales visible on leaves and twigs. Well-preserved seeds are black and shiny and have a short point near the apex, a notch to one side near the base, and a shallow, inconspicuous groove in between. Like the preceding species, *S. canadensis* is a shrub of calcareous mineral soils and open habitats (e.g., slopes, sandy shores, sparse spruce woodlands). It is distributed from Newfoundland to Alaska, and, in the East, south to Nova Scotia, central Maine, Vermont, and western New York. On the basis of fossil pollen, Richard (1974) established that *S. canadensis* was more widely distributed in Quebec during late glacial and early postglacial times than it is now. FIGURES 30, 64.

Ledum groenlandicum Oeder. Nine leaves, the margins revolute and brown-tomentose beneath; two capsules, one with four valves, the other with five, dehiscent from the base. *Ledum groenlandicum*, a common low shrub of boreal North America, occurs from southern Greenland to Alaska, and, in the East, southward (and often discontinuously in isolated peat bogs) to northern New Jersey, Pennsylvania, and Ohio. FIGURES 65–67.

Arctostaphylos Uva-ursi (L.) Sprengel. Eleven fruit stones or fruit stone halves, in one case two fruit stones fused together laterally. Fruits from a selection of herbarium specimens show that stones can be free or fused to form a partial or complete ring. Compressed laterally, the individual stones are wedge shaped in cross section and have a gap in the wall near the base of the dorsal suture. Represented by var. *coactilis* Fern. & Macbr. in the southern part of its range, *A. Uva-ursi* occurs from Newfoundland and Labrador to Alaska, south to Long Island, Virginia, western New York, and northern Illinois, on well-drained soils or on rocks.

Vaccinium uliginosum var. **alpinum** Bigelow. Numerous obovate or elliptic leaves, generally 1 cm. or less long, reticulate venation visible in

some; one seed, similar to those of *V. uliginosum* in size and shape and in having the testa comprised of linear cells with thin anticlinal walls. Seeds of *Vaccinium* are more or less elliptic in side view but with one long side convex and the other straight or concave. Seeds differ in size (although within one fruit, smaller, possibly aborted, seeds are present) and in shape (e.g., round to triangular in cross section). Cells of the seed coat may be long (most species of northeastern North America) or short (*V. angustifolium* Aiton, *V. vacillans* Torrey). Anticlinal walls of the testa may be thick (*V. Oxycoccos* L., *V. vacillans* Torrey) or thin. When wet, the thin, transparent outer periclinal wall bulges outward, but when dry the testa is reticulate or areolate. In the southeastern part of its range (northern New York and New England), *V. uliginosum* var. *alpinum* occurs mostly on summits of the higher mountains. Otherwise, it occurs widely throughout boreal America from Newfoundland to Alaska. FIGURE 68.

Compositae. Two achenes, of identical size and shape, a few pappus bristles present at the apex of one. We have not been able to identify the fossils more precisely, but their occurrence establishes the presence of reproducing plants of this predominantly herbaceous family. FIGURE 31.

Musci. Intermixed with macrofossils of vascular plants were well-preserved but small (generally less than 0.5 cm. long) leafy fragments of mosses. Although fossil Musci compose a minor part of the sieve residues, 32 species representing extant mosses have been identified. These form the basis of a separate study (Miller, unpubl. ms.) and are only briefly discussed here.

The moss assemblage contains no strictly arctic or subarctic species. Mosses now mostly northern in distribution are represented, however, and some occur well into the arctic zone. Only one, *Hygroamblystegium tenax* (Hedwig) Jenn., which in eastern North America ranges from Florida and Arkansas northward to southern Canada, could be termed a southern species. Other members of the assemblage, for example *Catoscopium nigritum* (Hedwig) Bridel, *Cratoneuron commutatum* var. *falcatum* (Bridel) Moenk., and *Scorpidium turgescens* (T. Jensen) Loeske, are widespread in the North but sporadic and local along the southern edge of their ranges, which may extend to the northern United States. Species with present-day disjunct eastern-western North American distributions are represented (e.g., *Timmia austriaca* Hedwig, *Tortella inclinata* (R. Hedwig) Limpr., and *Hypnum revolutum* (Mitten) Lindb., although the range of the last in North America has not been fully documented).

The assemblage consists almost entirely of species found in calcareous habitats. These include hygric phases of rich fens (*Drepanocladus revolvens* (Sw.) Warnst., *D. vernicosus* (Lindb. ex C. Hartman) Warnst.,

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FIGURES 61–68. Plant macrofossils from Columbia Bridge site. 61–63, *Elaeagnus commutata*: 61, 62, immature fruits, peltate scales visible as punctae; 63, ellipsoid, eight-ridged inner wall of calyx tube surrounding seed (from mature

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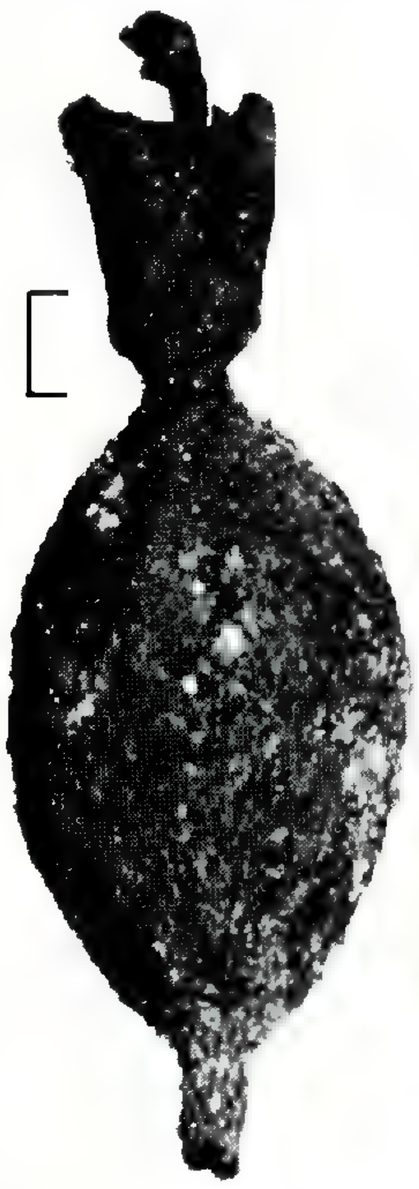

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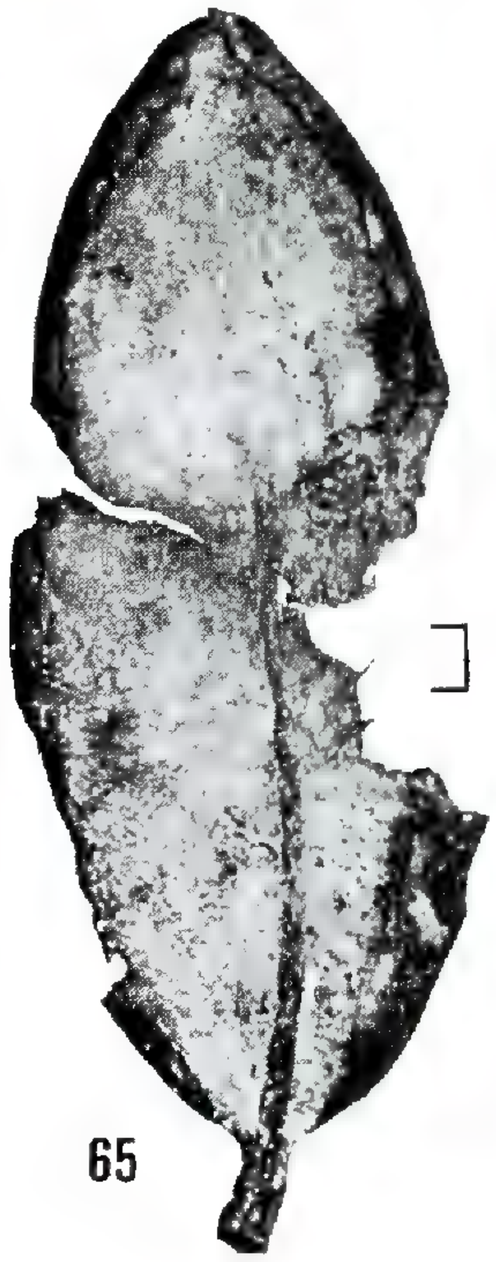

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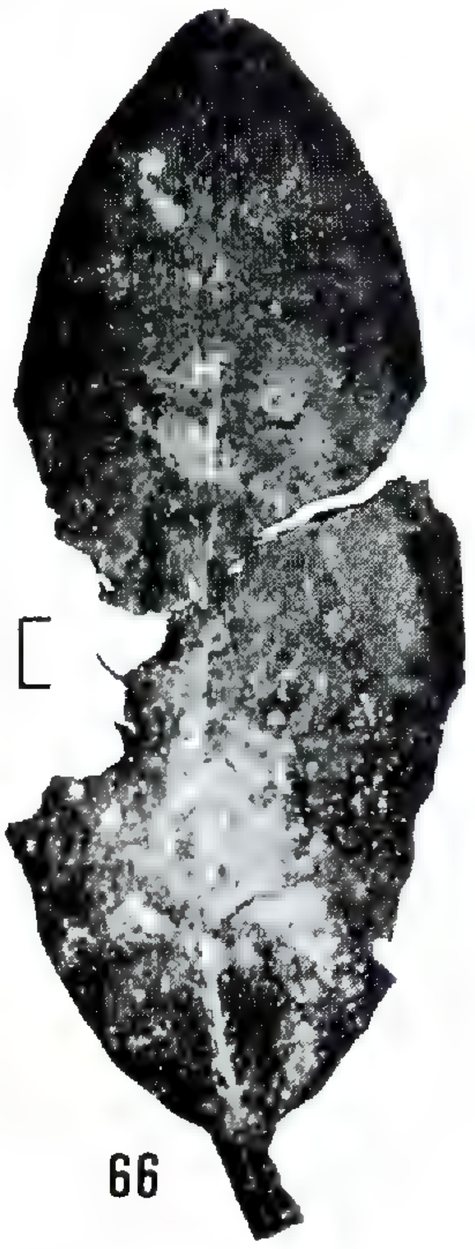

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fruit). 64, *Shepherdia canadensis*: two seeds. 65–67, *Ledum groenlandicum*: 65, leaf, lower surface; 66, same leaf, upper surface; 67, capsule. 68, *Vaccinium uliginosum* var. *alpinum*: three leaves, (from left) upper, lower, and upper surfaces. Scale lines = 1 mm.

and *Scorpidium turgescens* (T. Jensen) Loeske), calcareous seeps or streams (*Hygrohypnum luridum* (Hedwig) Jenn.), and moist to dry calcareous rocks or soil (*Ditrichum flexicaule* (Schwaegr.) Hampe, *Dicranella varia* (Hedwig) Schimper, *Hypnum vaucheri* Lesq.). While a few of the species represented can occur beneath forest cover, no characteristic forest species are present. Thus, the assemblage indicates the presence of several distinct wet to dry, nonforest communities rich in calcicolous species.

INTERPRETATION

RADIOCARBON AGE DETERMINATIONS

The age of the laminated sediments has been established by radiocarbon dating. Two of the dates were from wood fragments picked from the sediment. The upper, at 0.84 meter below the top of the deposit, is 11,390 ± 115 years B.P. ($\delta^{13}C = -27.5$ 0/00; WIS-919). The lower, at 1.52–1.58 meters, is 11,540 ± 110 years B.P. ($\delta^{13}C = -29.0$ 0/00; WIS-961). However, a block of sediment rich in organic matter from an intermediate depth, 1.36–1.45 meters, yielded an age of 20,500 ± 250 years B.P. (WIS-925). We reject this last date. The sediment submitted for dating was calcareous clay, silt, and sand containing abundant *Potamogeton* leaves, in addition to other plant remains. Donner *et al.* (1971) demonstrated that living plants of *Potamogeton* can give radiocarbon ages up to 3000 years old. During photosynthesis, aquatic plants can utilize carbon dioxide and carbonate and bicarbonate ions in solution that may contain carbon derived from ancient sediments. We conclude that this effect may be in part responsible for an age determination that is too old in relation to the other dates and to its stratigraphic position. However, the difference between the older and younger age determinations is greater than that attributable to the effect of "old" carbon. In view of the sedimentary setting of the deposit and the stratigraphic relation of the dated levels, we think that rebedded interstadial organic material is an unlikely cause. With the new ion counting technique of radiocarbon dating (see Stuiver, 1978), it may be possible to date associated wood fragments and leaves separately, and thereby to determine if they are of different age.

The radiocarbon ages reported here are the first to be determined directly for any lacustrine sediment in the Connecticut River valley. Consequently, they are important for a better understanding of the glacial history of New England. If the Columbia Bridge sediments are glaciolacustrine, these radiocarbon dates demonstrate that 11,500 years ago there was an ice margin in the upper Connecticut River valley drainage near the site. In Quebec, by 11,500 years ago an active ice margin had retreated to the St. Lawrence Lowland (Gadd *et al.*, 1972), and the Champlain Sea had been in existence for over 500 years (Cronin, 1977; Occhietti & Hillaire-Marcel, 1977). Thus, an ice margin in the upper Connecticut drainage at this same time would represent a local glacier, perhaps an active ice cap

or a long-lived stagnant mass of ice. Several workers (Flint, 1951, 1953; Schafer, 1968; Prest, 1969; Shilts, 1976) have proposed the existence of late glacial ice caps in the White Mountains and in other areas of northern New England. In the Thetford Mines area of Quebec, LaMarche (1971) reported evidence for late Wisconsinan north-flowing ice. Shilts (1976) concluded that ice flowed north and northwest from an ice mass stranded in the area of the international boundary in Maine and Quebec. In northwestern Maine, 128 km. northeast of Columbia Bridge, Hanson and Caldwell (1977) found end moraines and glacial striae that indicate ice flow southeastward from an ice cap stranded on the Boundary Mountains. They tentatively date these moraines at 11,000–12,000 years B.P., a time that postdates the marine invasion of the St. Lawrence Valley.

We conclude that the 11,500-year-old sediments at Columbia Bridge are glaciolacustrine. Their deformation indicates that they may have been deposited on or adjacent to a mass of stagnant ice. With the evidence at hand, we can not determine the character of the lake's dam, and we are uncertain at which end the valley was dammed. However, the presence of a glacial lake in the Upper Connecticut Valley between 11,000 and 12,000 years ago supports the hypothesis of a local glacier in northern New England and southern Quebec at that time.

Vegetation

Several lines of evidence are available for a reconstruction of vegetation and environments near the fossil site 11,500 years ago. Chief among these are the pollen spectra and plant macrofossils. Animal fossils in the deposit, which include molluscs, ostracods, and insects, are currently under study by various specialists, and paleoecological data from this work will supplement conclusions reached from an analysis of the plant remains.

Pollen Analyses

General. Before a botanical interpretation of the pollen assemblages is presented, two important influences that have modified the spectra will be discussed: 1) weathering, which is restricted to the upper part of the laminated sediment, and 2) the constant presence of deteriorated pollen and spores.

Evidence of oxidation in the laminated sediments above 0.75 meter has already been described. Oxidative degradation of the microfossils during weathering is the likely cause of differences between spectra near the top and bottom of the profile. Different kinds of pollen resist oxidation in varying degrees (Sangster & Dale, 1964). Among pollen or spore types represented in the sediments (Figure 2), *Pinus*, *Quercus*, *Carpinus-Ostrya*, Polypodiaceae, and Lycopodiaceae appear to have been the most resistant to *in situ* weathering; *Picea*, *Juniperus-Thuja*, *Corylus*, and Cyperaceae were less resistant; and *Abies* seems mostly to have been eliminated from

the weathered zone. Those types relatively unaffected by oxidation were *Fraxinus*, *Betula*, *Artemisia*, and high-spine Compositae.

The relatively constant proportion of deteriorated and unknown pollen and spores in sediments below 0.75 meter indicates continuous input of deteriorated grains. Most of these were degraded (*sensu* Cushing (1964)) since they had an abraded appearance or unresolvable exine stratification. Degraded pollen in late glacial lake sediments is generally interpreted as originating from till through redeposition (Cushing, 1964), but confirmation of this process may be difficult to obtain. Also, sediments of large lakes (according to Lougee (1939), Lake Colebrook was perhaps 35 km. long and up to 2 km. wide) have been found to contain a higher proportion of deteriorated and unknown grains than do sediments of small lakes (McAndrews & Power, 1973). This may be because larger lakes often have extensive watersheds, and pollen deposited in them spends time exposed to air on surrounding surfaces before being washed into the basin. Cushing (1964) called such pollen "penecontemporaneous" to distinguish it from pollen reaching a basin directly by air. Exines of pollen in and on soil are often distinctively corroded by microbial activity.

While it is not possible to determine accurately the size of the watershed that fed Lake Colebrook, to judge from deltaic deposits exposed in 1977 along the west side of the valley near the fossil site, it appears that tributary streams entered the lake. The lenses of organic detritus also indicate periodic input of terrestrial plant matter, perhaps by stream action. It is surprising, therefore, that no pollen showing evidence of microbial corrosion was observed during our counts. The reason for the absence of this type of deteriorated pollen is not known. Studies of even small lakes with tributaries (Peck, 1973) have shown that 90–96 percent of the pollen can be stream carried. Most stream-borne pollen presumably comes from nearby upland surfaces that contribute pollen accumulated in soils or other traps and by erosion of fossiliferous sediments and rocks. Although we cannot demonstrate a probable source, most of the deteriorated pollen and spores may possibly have been redeposited from till. Unfortunately, degraded and corroded grains are not always distinct microscopically, and the process of deterioration of pollen and spores on recently deglaciated surfaces has been poorly investigated.

The age of the degraded microfossils is unknown, but interstadial, interglacial, or even Tertiary deposits are possibilities. Among the unknown pollen grains in the sediments were some that resembled *Engelhardtia*, which is present in the early Tertiary Brandon lignite of west-central Vermont (Traverse, 1955). Grains resembling *Platycarya*, common in the Tertiary elsewhere, are also present. Late glacial inorganic lake sediment often contains these and other redeposited Tertiary microfossils (Iversen, 1936; M. Davis, 1961; Cushing, 1964, 1967), especially in areas of Tertiary bedrock. However, *Engelhardtia*- and *Platycarya*-like grains from the Columbia Bridge deposit cannot be positively identified because of poor preservation. These Tertiary pollen types are flattened, while most pollen and spores in our samples were inflated. Therefore, in the absence of any

definite and abundant Tertiary pollen types, we think that the redeposited microfossils are mostly from Pleistocene plants and are rebedded from Pleistocene sediments.

Percentages of various pollen types below 0.75 meter are relatively consistent from spectrum to spectrum, and these pollen assemblages form the basis of the vegetational interpretation discussed below. The assemblages could have been modified arithmetically by subtracting all deteriorated pollen from the totals, but this was not done because the percentage of deteriorated pollen is also more or less constant throughout the unweathered interval.

POLLEN SPECTRA BELOW 0.75 METER. Although there is evidence of rebedded pollen in the profile, spectra below 0.75 meter are nevertheless similar to assemblages from basal small lake and bog sediments at sites in northern New England and adjacent Quebec. Remarkably similar is the lower part of zone A at Brownington Pond, Vermont (M. Davis, 1965), 47 km. west of Columbia Bridge. At both sites pollen of *Picea* and *Pinus* are the most frequent types (ca. 40–50 percent), and *Juniperus-Thuja* and *Quercus* are the next most prominent. *Betula* percentages are low (5 percent or less). Pollen of herbs (mostly Cyperaceae) and shrubs total 30 percent. Spectra from zone 8 at Barnston Lake, Quebec (Mott, 1977), which is 37 km. northwest of Columbia Bridge, are also similar except for higher *Betula* and lower Cyperaceae percentages.

The radiocarbon age of the Brownington Pond sediments has not been reported, but the Barnston Lake spectra are dated at slightly older than 11,150 years B.P. Radiocarbon dates of 11,030 ± 200 and 11,290 ± 200 years B.P. have been reported for basal sediments of Bugbee Bog, Caledonia County, Vermont, 72 km. southwest of Columbia Bridge (McDowell *et al.*, 1971). The radiocarbon-dated interval at this site was not analyzed for pollen, but spectra from levels just above the dated interval in an adjacent core are dominated by pollen of *Picea* and *Pinus* with some *Betula* and *Salix* (Σ = total AP); percentages of Cyperaceae and other herbs are less than 1 percent (Σ = AP + NAP + spores). These spectra differ greatly from the Columbia Bridge assemblages. Whitehead and Bentley's profile (1963) from Pownal Bog in southwestern Vermont includes only a basal zone dominated by *Picea* with some *Pinus* and *Abies* but lacking an appreciable amount of herb or shrub pollen.

The detailed pollen diagram of R. Davis *et al.* (1975) from Moulton Pond in southern coastal Maine, 225 km. east of Columbia Bridge, includes a lengthy radiocarbon-dated interval that is in part contemporaneous with deposition of the Columbia Bridge laminated sediments. Spectra of similar age from the two localities correspond fairly closely. The principal differences include somewhat larger percentages of *Betula*, *Alnus*, and Gramineae, the presence of *Myrica*, and the absence of *Juniperus-Thuja* at Moulton Pond.

R. Davis *et al.* (1975) review the evidence that such pollen assemblages represent tundra vegetation. This includes similarity between percentage

composition of surface pollen accumulations in present-day areas of tundra and fossil spectra and also corresponding pollen influx values, i.e., a similar number of grains deposited/cm.^{2}/year.

Pollen assemblages with large relative amounts of Cyperaceae pollen (ca. 20 percent) in association with *Picea* (ca. 30 percent), *Pinus* (ca. 15 percent), and lesser percentages of *Betula*, *Alnus*, *Salix*, and Gramineae are being deposited today in the tundra and tundra-forest ecotone of northern Quebec and Labrador (R. Davis & Webb, 1975). Columbia Bridge spectra differ somewhat from the current pollen rain of that region in having slightly less *Alnus* and *Betula*, as well as in including *Quercus* and other Temperate Zone deciduous trees. In eastern North America the consistent occurrence in late glacial sediments of pollen of *Quercus*, *Acer*, *Carya*, *Carpinus* and/or *Ostrya*, and other thermophilic trees is a well-known but puzzling phenomenon. That trees of these genera were in fact established on the late glacial landscape has not been demonstrated by macrofossil finds. This pollen may thus either represent rebedded contaminants or have been carried by air from a distant source. Even though present in low concentration, such wind-blown pollen becomes prominent in percentage data if the parent vegetation is characterized by low pollen influx. At Moulton Pond influx values during the presumed tundra phase varied from 150 to 920 grains/cm.^{2}/yr. This is well within the range of influx reported by Ritchie and Lichti-Federovich (1967) for tundra sites in arctic North America and is also among values calculated by R. Davis and Webb (1975) for other New World tundra localities.

If it is assumed that the Columbia Bridge rhythmites are varves, pollen influx at the site 11,500 years ago was 4600 to 6600 grains/cm.^{2}/yr. (TABLE 2). Tributary-fed Lake Colebrook perhaps accumulated sediment with a low airborne component, as do comparable modern small lakes that contain 4–10 percent pollen deposited out of air (Peck, 1973). If true, this reduces influx to 184 to 660 grains/cm.^{2}/yr. Influx determinations of pollen deposited in open Petri dishes at tundra localities in the New World Arctic (Ritchie & Lichti-Federovich, 1967) vary from 5 to 762 grains/

TABLE 2. **Pollen and spore concentration and influx.**

DEPTH (m.)	POLLEN AND SPORE CONCENTRATION (number/cc.)	RHYTHMITE THICKNESS (cm.)	INFLUX (number/cm.^{2}/yr.)
0.0–0.05	67	1.20	81
0.20–0.25	165	2.04	336
0.50–0.55	889	1.56	1387
0.80–0.85	1470	3.24	4765
1.10–1.15	2774	2.38	6603
1.35–1.40	3322	1.73	5747
1.55–1.60	2174	2.13	4631

cm.^{2}/yr. ($\overline{X}$ = 200). Influx values of from 2000 to 3000 grains/cm.^{2}/yr. are also within the range of values reported for tundra localities by other workers (M. Davis *et al.*, 1973) or correspond to measurements taken in the boreal forest-tundra ecotone (R. Davis *et al.*, 1975, *t. 1*), where trees are sparsely represented. Thus, both pollen percentages and pollen influx data from the Columbia Bridge deposit indicate that the landscape was essentially treeless in the area of the site 11,500 radiocarbon years ago.

Apart from Moulton Pond, evidence of late glacial tundra in sediments at other sites near the Columbia Bridge deposit has been reported by Mott (1977) and Richard (1977). Zone 8 at Barnston Lake was interpreted by Mott (1977) as representing tundra, which at this locality was replaced by taiga 11,200 years B.P. Following a detailed regional study of sites north and south of the St. Lawrence River, Richard (1977) recognized a tundra phase that existed from 11,500 to 11,000 years B.P. at localities close to northern New England. Palynological evidence of tundra is present in Richard's Mont Shefford and Albion profiles (Richard, 1977), which are 105 km. northwest and 118 km. north of Columbia Bridge, respectively. Arboreal pollen types at these two sites range between 40 and 70 percent during the tundra phase, but pollen concentration values are high (ca. 10,000 to 75,000 grains/cc.). Influx determinations are not available for the sites.

In older sediments at Mont Shefford and Albion, pollen concentration values are much lower and approach those recorded at Columbia Bridge. Richard (1977) has interpreted these older sediments as containing a record of "periglacial desert" in which herbs and lichens occurred sparsely on the landscape prior to development of a more continuous cover of vegetation during the succeeding tundra phase.

Macrofossils

The occurrence of plant macrofossils at Columbia Bridge permits an evaluation of the periglacial desert hypothesis and also of the more general interpretation that low pollen influx and high herb and shrub to tree pollen ratios indicate a treeless, tundra-type vegetation. The abundance and diversity of plants recovered as macrofossils indicate the presence of a rich flora comprised of species that presently grow in a variety of habitats. Most of the species are herbs or low-growing shrubs. The landscape appears to have supported relatively few trees, and these were spruce (*Picea* sp.) and balsam poplar (*Populus balsamifera*). It is not possible to decide whether these occupied positions on exposed upland slopes or in sheltered places along streams and valleys in the adjacent upland. Balsam poplar is a fast-growing tree that pioneers in disturbed areas along streams and rivers in the present-day boreal forest. Species of spruce are also common colonizers of recently disturbed mineral soils.

The macrofossils also permit more precise identification of species in the flora than otherwise would be possible from pollen alone. Pollen of *Juniperus* and *Thuja* (Cupressineae of many pollen analysts) is so similar

as to be essentially indistinguishable in the fossil condition. At Columbia Bridge *Juniperus-Thuja* pollen is most certainly of *Juniperus communis* because abundant macrofossils of this species, including a microsporangiate strobilus, occur in the deposit. The status of *Populus* in late glacial sediments is uncertain because its pollen may be difficult to identify and, in fact, is not always preserved. Mott (1978) has recently redrawn attention to these problems and, with new data, concluded that *Populus* perhaps had a significant role during the change from tundra to forest. For eastern North American sites some workers indicate that *P.* cf. *tremuloides* (Richard, 1977; identification based on pollen) was the species involved; others suggest *P. balsamifera* (M. Davis, 1958; identification based on pollen). At Columbia Bridge the poplar present was *P. balsamifera*. Macrofossils of the various identified species of *Carex* and *Salix* and of *Betula* similarly help to define the late glacial flora. However, determination of how widespread the identified species in these genera may have been 11,500 years ago must await discovery of macrofossils at additional sites.

Apart from the pondweeds, *Potamogeton filiformis* and *P. pusillus*, which grew submerged, probably along the shore of Lake Colebrook or in shallow ponds drained by waters flowing into the lake, no other aquatic seed plants are represented in the macrofossil assemblage. However, *Carex aquatilis* is a plant of wet habitats. *Selaginella selaginoides*, *Ranunculus Cymbalaria*, and a few other species grow on moist soil among rocks near running or stationary water. Remaining members of the vascular plant assemblage are plants of better-drained sites, and these species may form a fair sample of the flora that grew on upland, nonaquatic surfaces. The moss assemblage can similarly be divided into a species group typical of wet habitats and another of drier sites. Aquatic and semiaquatic species are best represented in the moss assemblage, indicating that the landscape near the fossil site was provided with a variety of wet habitats such as rich fens, fen margins, seeps, and streamsides. Drier sites interspersed among these, including ridgetops and slopes, upland bedrock areas, gravel bars along tributary streams, and beach deposits, are indicated by nonaquatic members of both moss and vascular plant macrofossil assemblages.

The lack of soil maturity or the presence of periodically disturbed sites is indicated by the abundant occurrence in the deposit of *Dryas Drummondii*, which is a pioneer on calcareous river-gravels, talus slopes, and bluffs. At the present time in lowland areas along rivers of the Gaspé Peninsula, this species and balsam poplar are conspicuous associates. *Dryas integrifolia*, *Saxifraga aizoides*, *Sibbaldia procumbens*, and other seed plants in the assemblage can also pioneer in suitable habitats. In certain currently glaciated areas, for example at the terminus of the Athabasca Glacier in Alberta, *Dryas Drummondii* and *Saxifraga aizoides* are among the first conspicuous angiosperms to become established on the moraines.

Species represented in the macrofossil assemblages are of ecological interest from two other standpoints. Nearly all are calcicoles. Among the identified seed plants for which such information exists, only *Betula glandulosa*, *B. pumila*, *Silene acaulis* var. *exscapa*, *Sibbaldia procumbens*, *Ledum groenlandicum*, and *Vaccinium uliginosum* var. *alpinum* show current pref-

erences for acidic substrata. The list of mosses in this category is shorter. The significance of this observation will be discussed further under the heading "phytogeography," but the raw, recently exposed drift and bedrock surfaces near the fossil site must have been predominantly calcareous. Four members of the macrofossil assemblage, *Dryas integrifolia*, *D. Drummondii*, *Elaeagnus commutata*, and *Shepherdia canadensis*, through the activity of an endophyte in root nodules, have the capacity for nitrogen fixation (Silvester, 1977). A fifth, *Alnus*, may also have been present, although there is only palynological evidence for its occurrence. Nitrogen-fixing plants play an important role in enriching raw glacial soils (Lawrence *et al.*, 1967).

In summary, both pollen and macrofossil data indicate the presence of an essentially nonforested landscape in the Columbia Bridge area 11,500 years ago. Floristic diversity was high. Many kinds of herbs or low woody plants of herbaceous habit were represented, some of which have current arctic-alpine distributions. Thickets of low shrubs (*Betula*, *Salix* spp., *Elaeagnus*, *Shepherdia*) were present, as was some balsam poplar and spruce. A mixture of well- and poorly-drained habitats was available to support the species of mosses and seed plants represented, which have diverse edaphic requirements.

Phytogeography

The Columbia Bridge fossil plant assemblage consists of species that at the present time are broadly northern in distribution. While some of the plants now occur well into the Subarctic and Arctic, the entire assemblage does not strictly qualify as an arctic one. Nevertheless, certain of the species, including *Salix Uva-ursi*, *Betula glandulosa*, *Oxyria digyna*, *Silene acaulis* var. *exscapa*, *Saxifraga aizoides*, and *Sibbaldia procumbens*, are present members of an arctic-alpine element in the flora of the northeastern United States. These plants are currently of restricted distribution in the New England area. For example, *Oxyria digyna* and *Sibbaldia procumbens* are presently found only on Mt. Washington, New Hampshire, in alpine habitats (Pease, 1964) such as Tuckerman and Huntington ravines and the Great Gulf. *Silene acaulis* var. *exscapa* is similarly restricted to the summit areas of Mt. Washington and Mt. Katahdin, Maine. Of more general alpine distribution are *Salix Uva-ursi* and *Betula glandulosa*, which occur on a number of the higher mountain summits of Vermont, New Hampshire, and Maine. The low elevation occurrence of fossils of these alpine species is consistent with the hypothesis that the alpine flora developed from populations of arctic and subarctic plants that lived at many different elevations during the waning phases of glaciation (see Fernald, 1907). Restriction to mountain summits occurred as the lowlands become climatically and/or edaphically unsuited to continuation of populations at all elevations.

The present-day localization of arctic-alpines in New England and southeastern Canada was first discussed and evaluated in detail in Fernald (1907), who noted that arctic and subarctic disjuncts in this region could

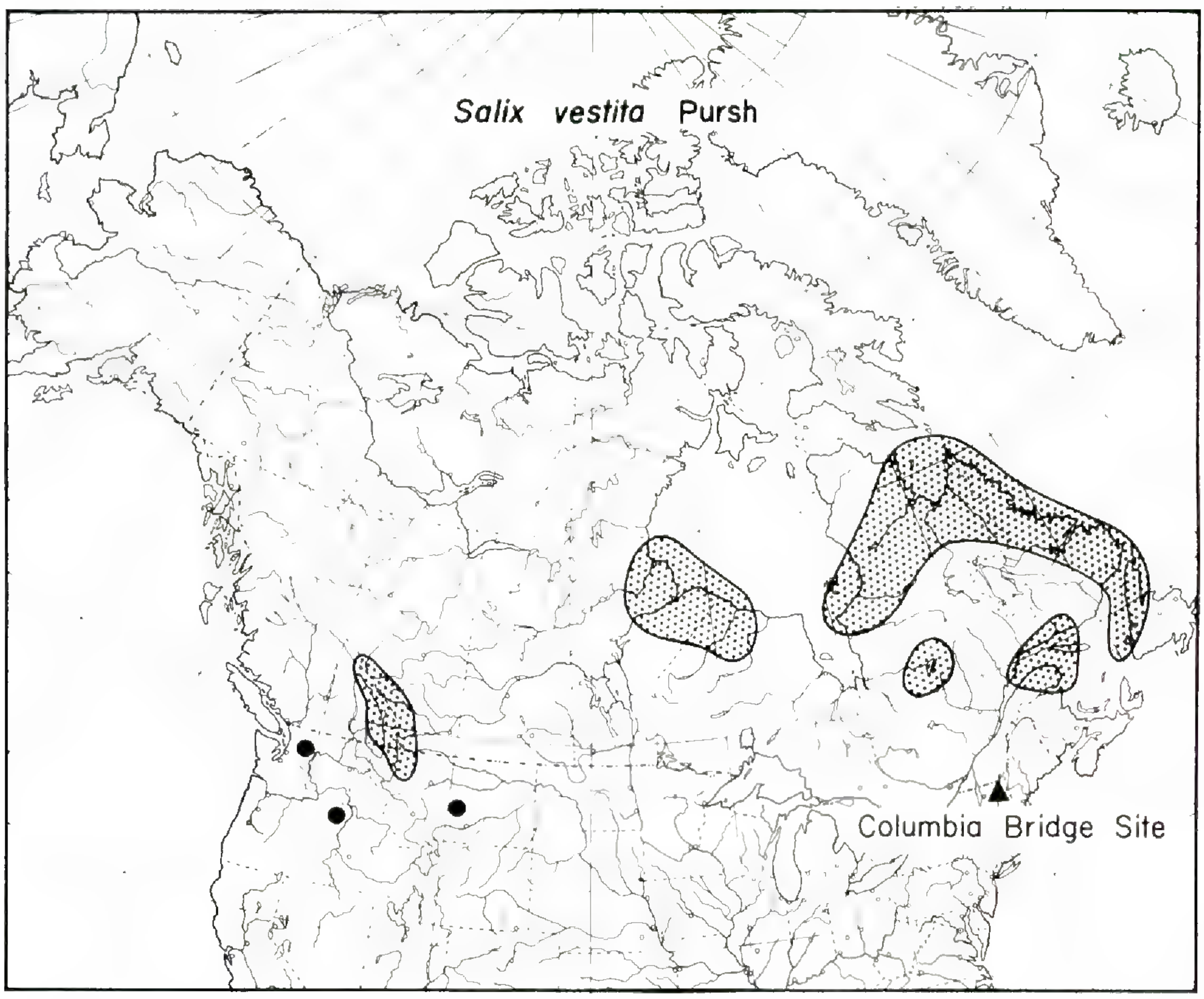


FIGURE 69. North American distribution of *Salix vestita* based on maps in Fernald (1925) and Raup (1943, 1959), specimens in A and GH, and data of Hitchcock and Cronquist (1964). Additional localities in Montana are given by White (1956). Triangle shows location of Columbia Bridge site.

be grouped into three categories that correspond to areas of acidic, calcareous, or serpentine rock. Alpine species of acidic soil preference are mostly restricted to the highest mountain summits (e.g., Mt. Mansfield, Vermont; Mt. Washington and nearby peaks; Mt. Katahdin), the coastal cliffs of eastern Maine, and Mont Jacques Cartier and vicinity on the Gaspé Peninsula, Quebec. Serpentine rock is rare in mountain areas of New England but occurs on the Gaspé (Mont Albert tableland). Localized areas of calcicolous alpine plants do not coincide with the highest elevations in New England, presumably because calcareous bedrock is absent from high alpine areas. Places rich in calcicoles include such low and moderate elevation areas as Smuggler's Notch on the east flank of Mt. Mansfield, the Willoughby Cliffs in northern Vermont, river cliffs of northern Maine and adjacent New Brunswick, sea cliffs along the north and east Gaspé coasts, and river bluffs and mountain spurs of interior Gaspé.

Subsequent floristic work in New England and regions immediately to the north have upheld Fernald's conclusions about the localization of alpine plants. Fossils from the Columbia Bridge deposit are of species that belong to his acidic and calcareous groups; no fossils of species in the shorter list of serpentinicolous plants were found. The association of

plants exhibiting different current soil preferences indicates the existence of ecologically diverse mixtures of species during late glacial time. In view of present-day restriction of alpine plants and the prevailing theory that called for northward migration of the boreal flora following ice withdrawal, Fernald (1907) had difficulty accepting that plants with such specific edaphic requirements could have grown together during the time of northward migration. He resolved the dilemma by supposing that raw glacial soils, having been brought together from a variety of sources, presented required nutrients in amounts that permitted heterogeneous mixtures of species to coexist. This hypothesis is attractive, but it ignores the possible role of competition, the lack of which prior to the establishment of forest cover, and on unstable, regularly rejuvenated surfaces, may have allowed unusual species associations to become established, particularly if the plants involved were pioneers. The absence of competition from trees is considered significant in explaining the presence of disjunct plants on soils of high base status in parts of Britain (Pigott & Walters, 1954). The same phenomenon helps to account for the localization of calcicolous plants on calcareous cliffs and ledges in the New England area where they form "islands" surrounded by communities of different composition.

Among the plants represented in the Columbia Bridge deposit the fol-

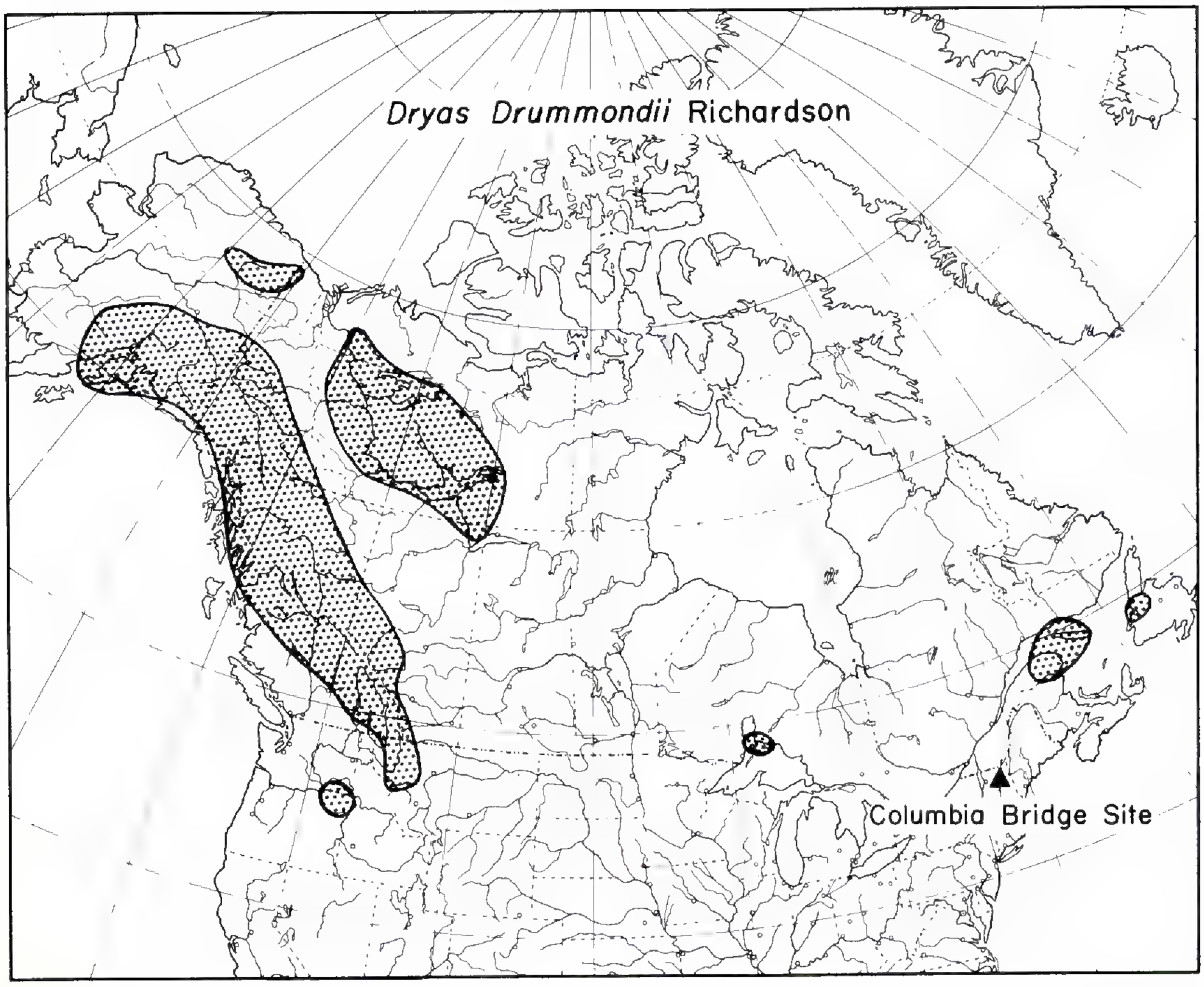


FIGURE 70. North American distribution of *Dryas Drummondii* based on maps in Hultén (1968), Rouleau (1956), and C. Rousseau (1974). Triangle shows location of Columbia Bridge site.

lowing are considered calciphiles (Fernald, 1907): **Selaginella selaginoides*, **Juniperus communis* var. *montana*, *Salix vestita*, **Saxifraga aizoides*, *Parnassia Kotzebuei*, *Dryas integrifolia*, *Dryas Drummondii*, **Shepherdia canadensis*, and *Elaeagnus commutata*. Only those preceded by an asterisk are members of the present flora of New England, and most of these are known from only a few localities (Seymour, 1969). The following Columbia Bridge plants are species of acidic soils (Fernald, 1907), and all are present members of the New England flora (Seymour, 1969): *Salix Uva-ursi*, *Betula glandulosa*, *Oxyria digyna*, *Silene acaulis* var. *exscapa*, *Sibbaldia procumbens*, *Ledum groenlandicum*, and *Vaccinium uliginosum*. All are strictly alpine except *Ledum*, which also grows at low elevations in acid peatlands.

In addition to species that exhibit arctic-alpine affinities, other members of the Columbia Bridge assemblage represent species that exemplify the well-known western-eastern North American disjunct pattern. These are: *Salix vestita* (FIGURE 69), *Parnassia* cf. *Kotzebuei*, *Dryas Drummondii* (FIGURE 70), and *Elaeagnus commutata* (FIGURE 71). The place nearest Columbia Bridge where these plants are now found is the Gaspé Peninsula, the present flora of which (Scoggan, 1950) contains all species we identified from the Columbia Bridge beds except *Polygonum ramosissimum*. On floristic grounds, therefore, it seems possible that the present Gaspé flora could in part have been derived from plant populations that no longer exist in northern New England and that might trace back in time and space to even more southern populations.

The region bordering the Gulf of St. Lawrence has long been known to harbor many examples of plants narrowly or broadly disjunct from occurrences in parts of western North America, most notably the northern Rocky Mountain area. Fernald (1925), whose field work in Gaspé and Newfoundland led to the early documentation of this pattern, suggested that the eastern populations persisted through glacial periods in refugia that were untouched by glaciation. These refugia were located essentially where the plants now occur in the East. Fernald's hypothesis, which was consistent with the geological and botanical evidence of the day, stimulated much discussion and research, and this has been summarized most recently by Drury (1969; see also Morisset, 1971), with emphasis on the Gulf of St. Lawrence region. Ives (1974) has also reviewed the extensive literature relating to the various ice-free refugia proposed for northern North America and Europe.

Discovery of intermediate stations during the past fifty years makes the eastern North American populations appear much less isolated than they initially seemed to be. For example, Drury (1969) reduced to 45 a list of 532 disjunct species and varieties published by Fernald in support of his hypothesis of unglaciated refugia. Also, there is agreement on geological evidence of glaciation in proposed nunatak areas near the Gulf of St. Lawrence, although the age of the glacial scouring and erratics remains unknown (Drury, 1969). Rousseau (1953), whose work in northern Quebec resulted in the discovery there of many of the "western" North

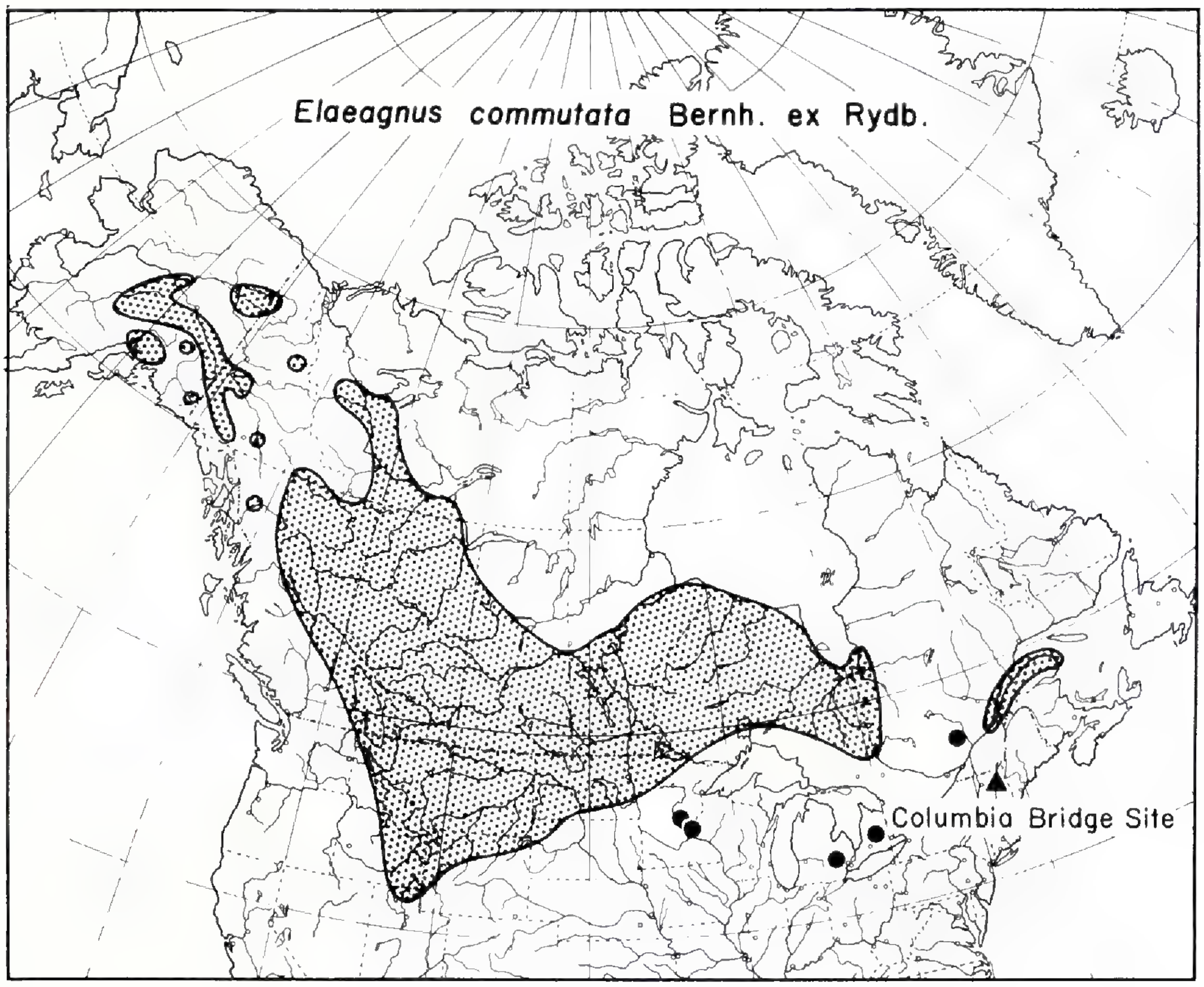
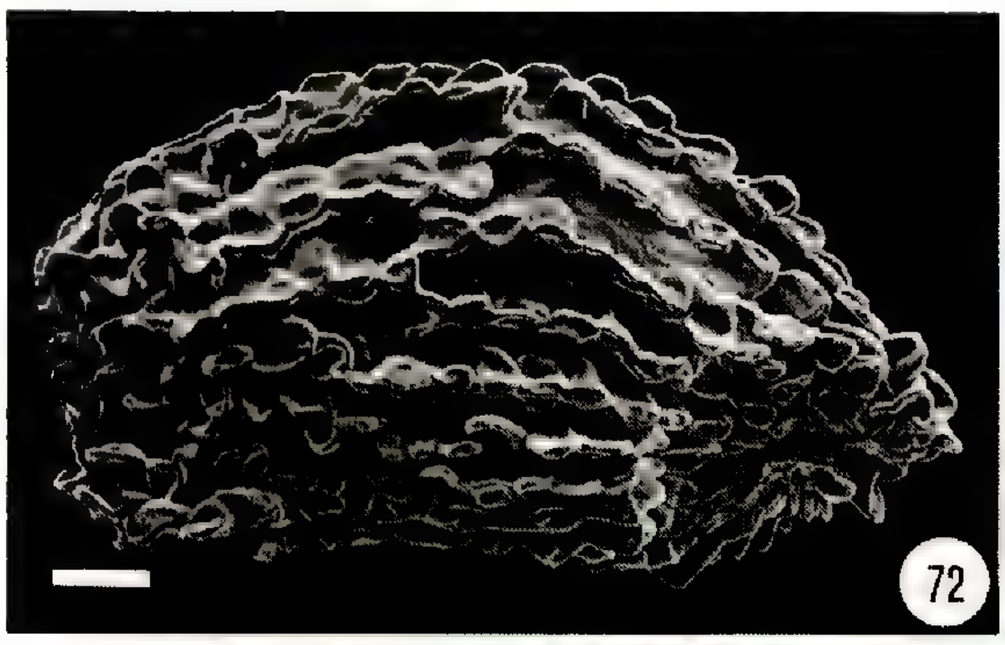
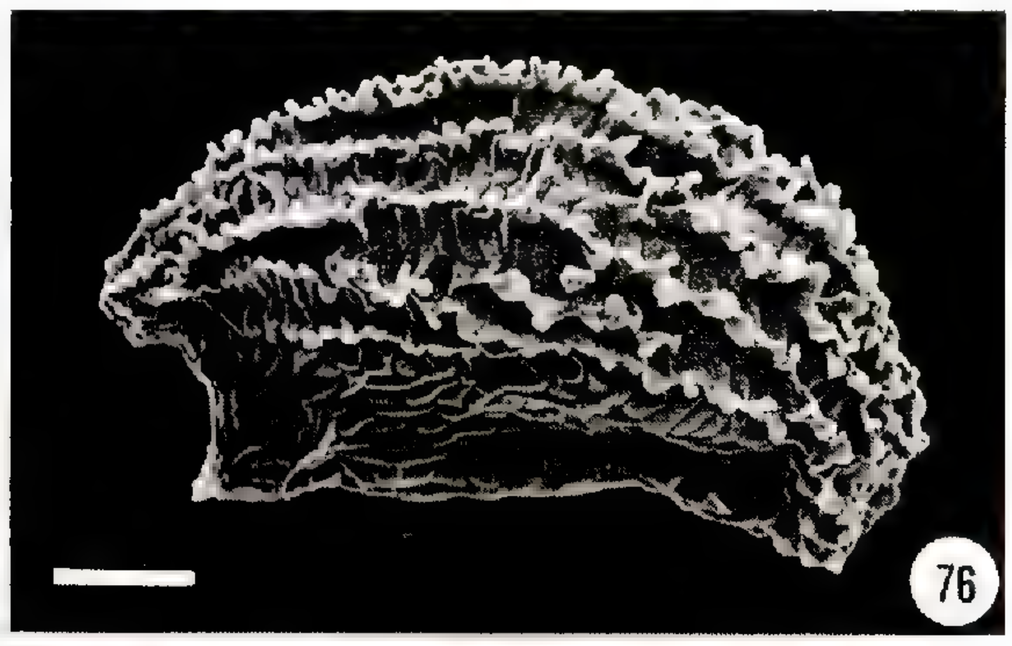


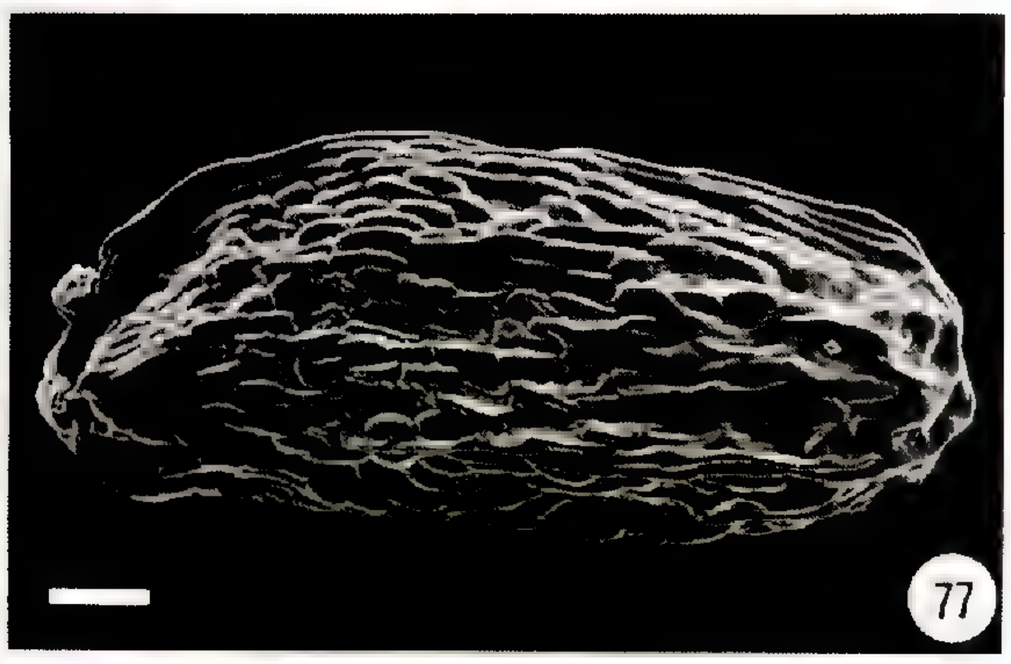
FIGURE 71. North American distribution of *Elaeagnus commutata* based on maps in Hultén (1968) and C. Rousseau (1974). Dots show locations of late Wisconsinan pollen records (Andersen, 1954; Birks, 1976; Cushing, 1967; Sigleo & Karrow, 1977; dot in Quebec refers to three sites in Mauricie National Park where *E. commutata* pollen occurs in late and postglacial sediments, data courtesy of P. Richard, University of Montreal). Triangle shows location of Columbia Bridge site.

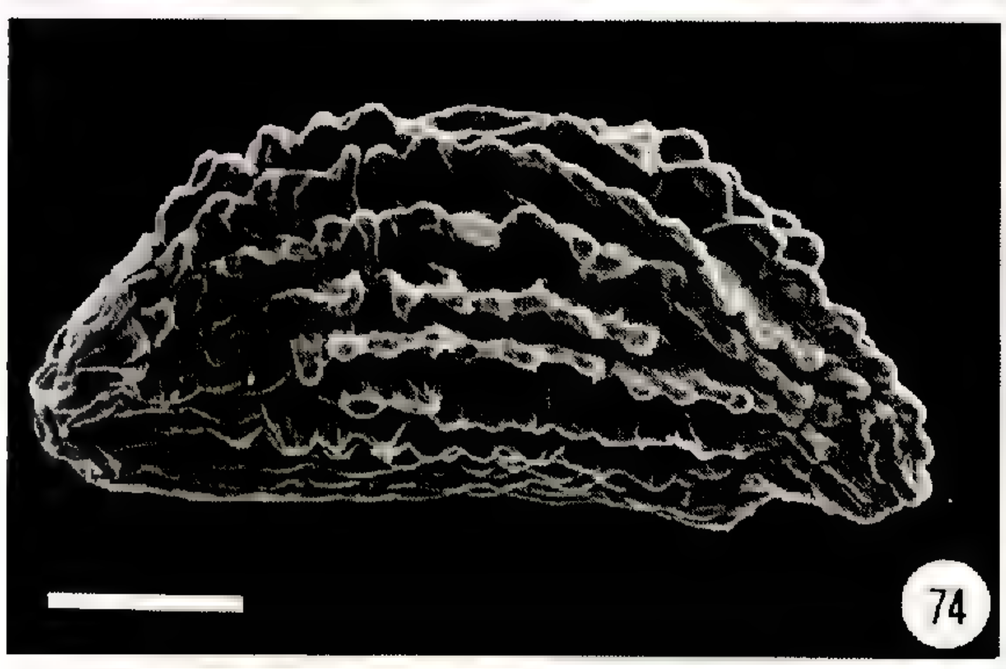
American species listed by Fernald, has proposed an alternative to the nunatak hypothesis, namely that as Quaternary glaciers receded, an "arctic corridor" adjacent to the ice sheet provided suitable conditions for eastward migration of species. Rousseau related the present occurrence of "western" plants on the Gaspé to postglacial colonization and persistence in suitable habitats. Thus, in Rousseau's view, the plants were late glacial relicts, whereas Fernald considered them relicts of preglacial times.

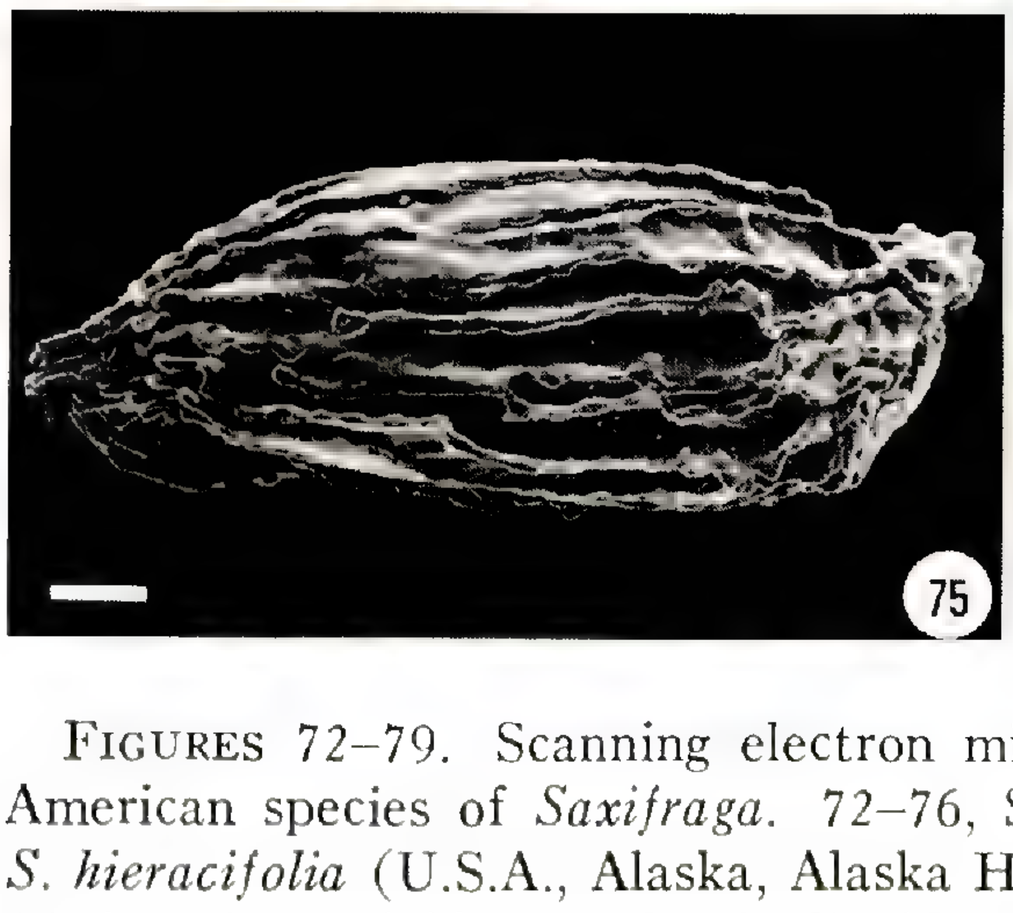
Few paleobotanical data have been cited in support of either hypothesis. However, the Columbia Bridge fossils show that at least some western-eastern North American disjuncts were present in eastern North America on recently deglaciated terrain during late glacial time. One of these, *Elaeagnus commutata*, which is distributed almost continuously from western to eastern North America, has other late glacial occurrences (FIGURE 71) beyond its present range, suggesting that the gap may be of recent origin. The Columbia Bridge fossils generally support Rousseau's hypothe-

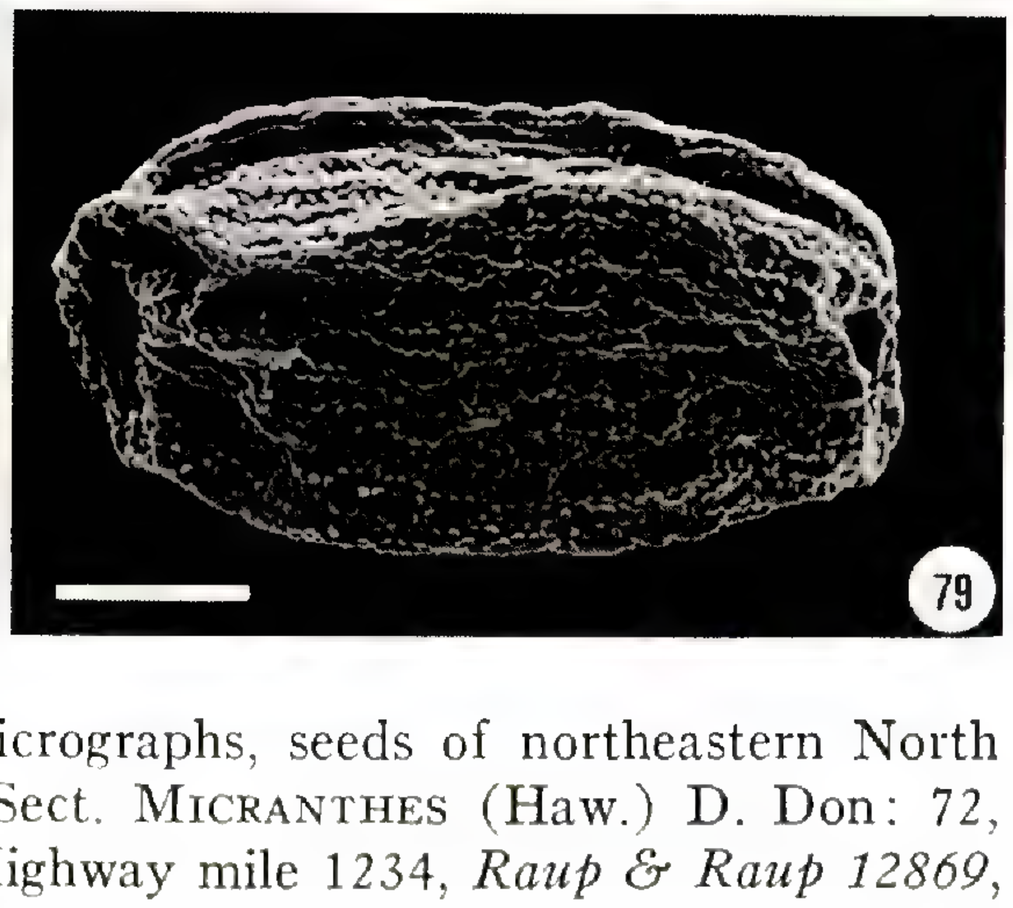












FIGURES 72–79. Scanning electron micrographs, seeds of northeastern North American species of *Saxifraga*. 72–76, Sect. MICRANTHES (Haw.) D. Don: 72, *S. hieracifolia* (U.S.A., Alaska, Alaska Highway mile 1234, *Raup & Raup 12869*, 16 Aug. 1944 (A)); 73, *S. nivalis* (Canada, Québec, e. coast Hudson Bay, Flaherty Island, *Abbe & Abbe 4093*, 30 Aug. 1939 (GH)); 74, *S. virginiensis* (U.S.A., New Hampshire, Coös Co., summit of Crag, *Deane s.n.*, 28 May 1919 (GH)); 75, *S. pensylvanica* (U.S.A., Massachusetts, Plymouth Co., Plymouth, *Boott s.n.*, 23 Sept. 1853 (GH)); 76, *S. stellaris* (Greenland, Sukkertoppen District, 65°25′ N., 52°41′ W., *Porsild 8063*, 4 Aug. 1940 (GH)). 77, 78, Sect. HIRCULUS Tausch: 77, *S. Hirculus* (U.S.A., Alaska, Kotzebue Sound, *Scamman*

sis of late glacial migration and establish that some of the "western" species cited by Fernald as indicating iceless refugia were in fact present on glaciated surfaces south of their areas of present occurrence.

It seems possible that edaphic and climatic conditions during late glacial time may have been appropriate for rapid plant migration, not only from west to east but in the opposite direction and, of course, from south to north. The fossil record must be more complete before the details of these migrations can be worked out. Within glaciated North America the western-eastern pattern of plant disjunction may be a result of postglacial range disruption in species that achieved transcontinental distributions during late glacial time. Eastern or western populations may also have had a history in either or both regions that predates the period of final ice withdrawal, as is the case with *Elaeagnus*, whose pollen (Sigleo & Karrow, 1977) occurs in a late Wisconsin interstadial deposit in Ontario (FIGURE 71). For glaciated regions the best approach to the problem of how ranges of plants developed is clearly to acquire a detailed record based on fossils.

SUMMARY

Rhythmically laminated sediments from the upper Connecticut River valley near Columbia Bridge have been radiocarbon dated at 11,390 ± 115 and 11,540 ± 110 years B.P. The deposit has been interpreted as glaciolacustrine, suggesting that a local glacier was present in northern New England at the time the sediments accumulated. The continental ice-sheet margin was in the St. Lawrence River valley 11,500 years ago.

Pollen and plant macrofossils from the sediments indicate that, although the landscape near the fossil site was predominantly treeless, a diverse flora of mosses, herbs, woody plants of herblike habit, and shrubs was established. Spruce and balsam poplar are minor components of the fossil assemblage. The mosses are nearly all species of wet to dry calcareous habitats, but both calcicolous and noncalcicolous seed plants are represented. This suggests that the absence of competition from trees and soil immaturity may have allowed heterogeneous associations of species to exist. Many of the seed plants are pioneers, and some play an important role in the revegetation of deglaciated terrain in areas of current alpine glaciation. The fossil assemblage includes *Dryas* (2 species), *Elaeagnus*, and *Shepherdia*, which, by virtue of nitrogen-fixing symbionts, presumably helped to enrich the raw glacial soils.

On the basis of identified macrofossils, the Columbia Bridge flora was broadly northern in composition. It consisted of arctic-alpine species (all of which are presently very rare in New England), boreal and subarctic

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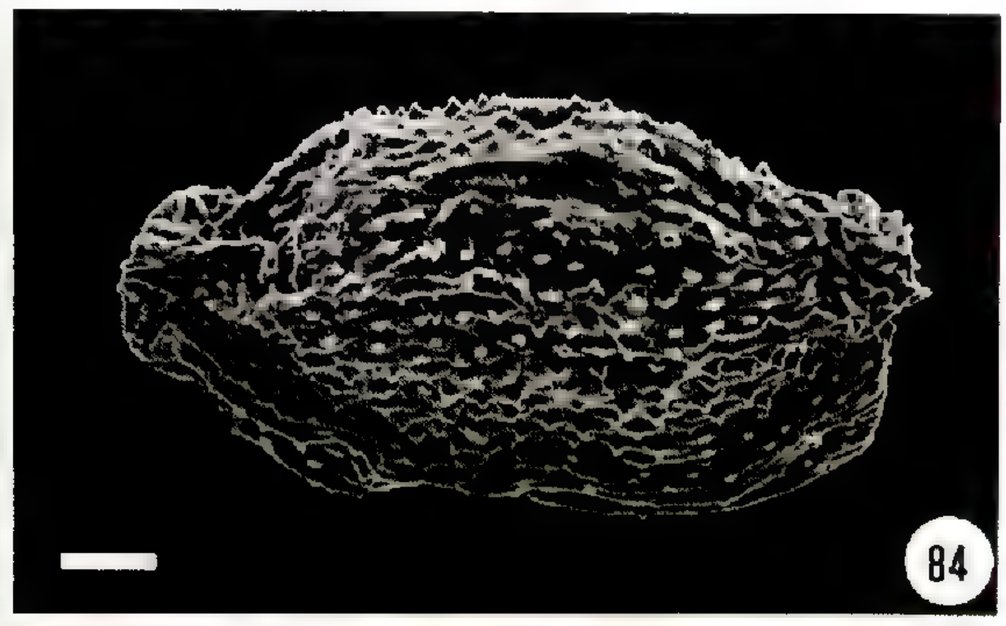
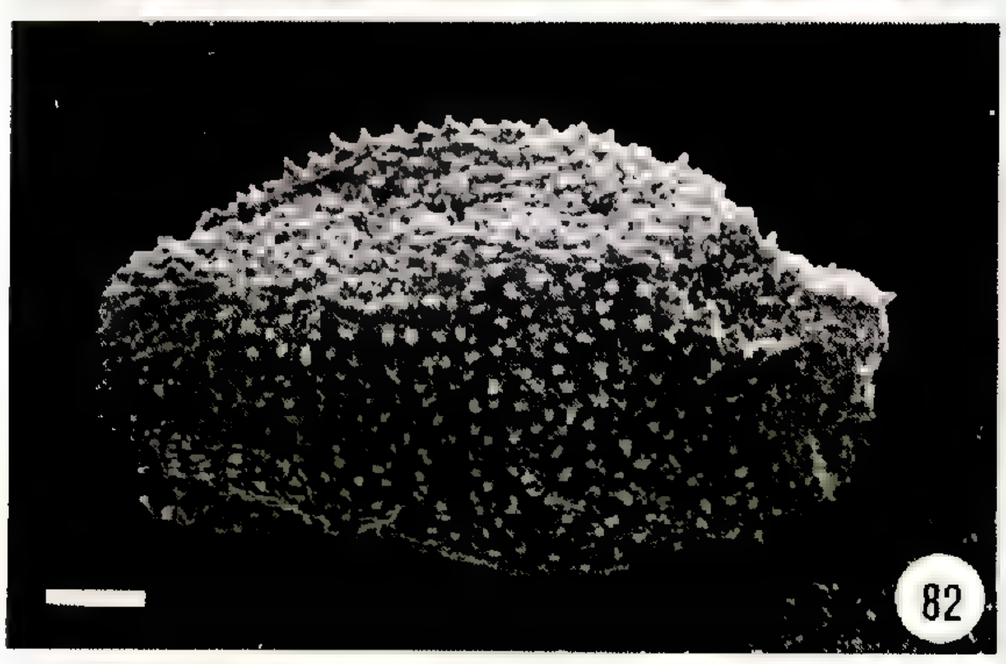
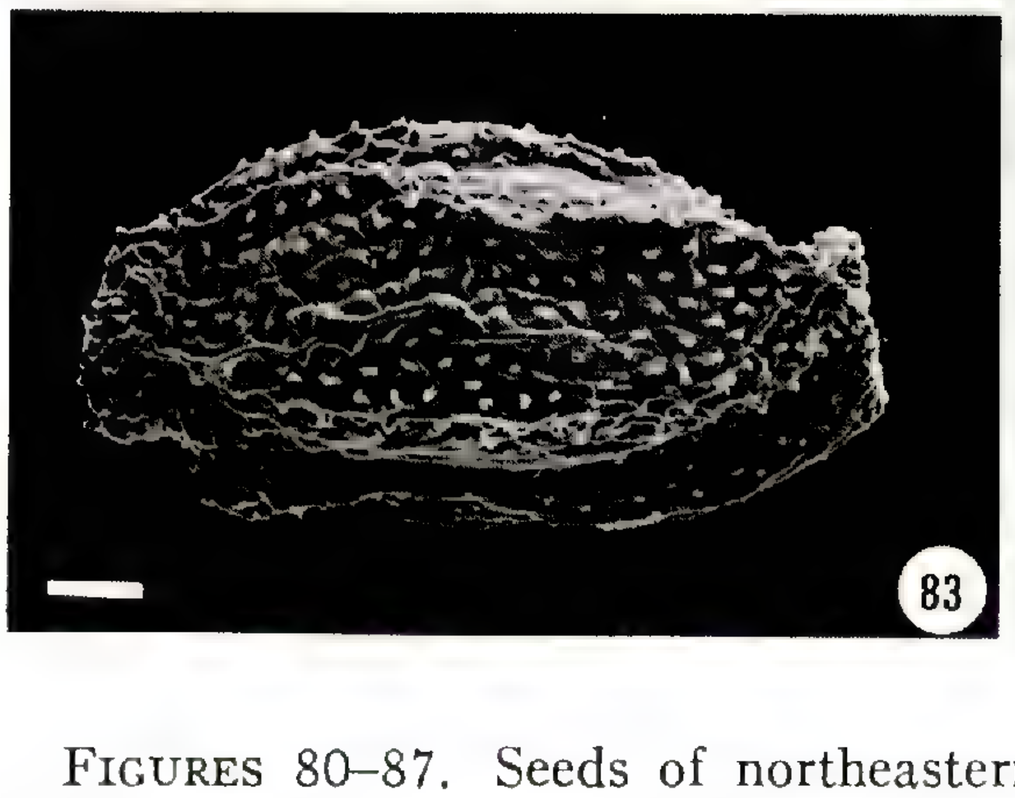
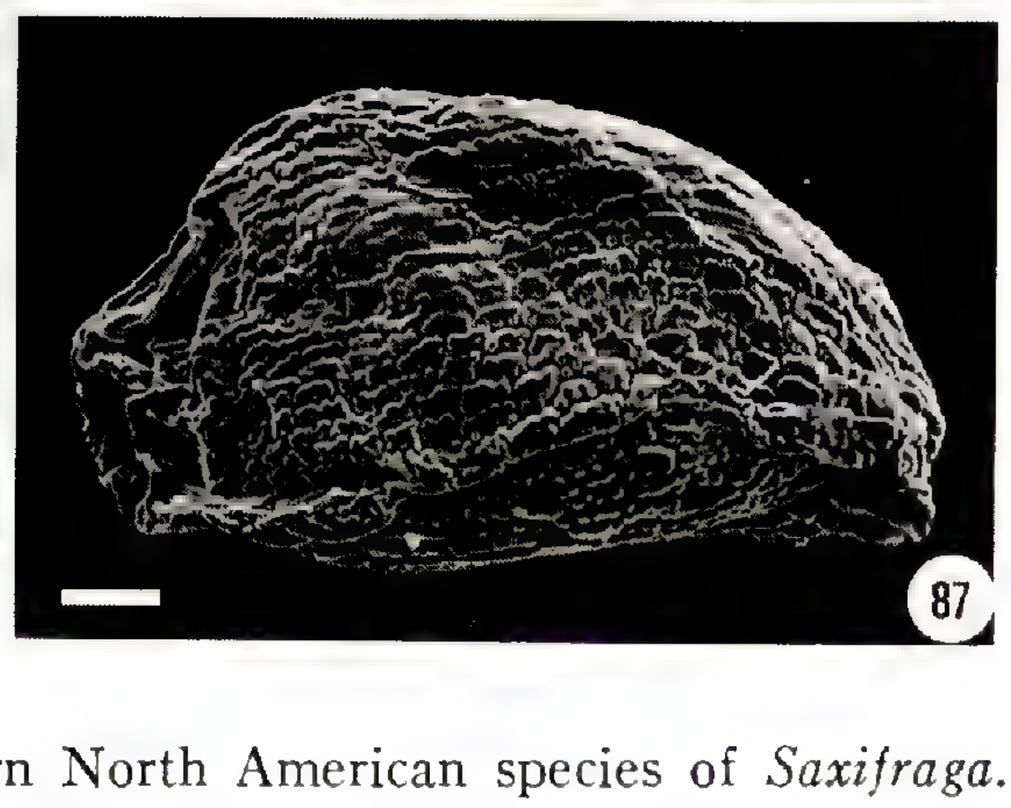
6466, 17–27 Aug. 1951 (GH)); 78, *S. flagellaris* (Canada, N.W.T., e. slope Richardson Mts., 68° N., 136° W., *Porsild 6828*, 15–17 Aug. 1933 (GH)). 79, Sect. SAXIFRAGA: *S. rivularis* (Canada, N.W.T., e. slope Richardson Mts., west Mackenzie River delta, *Porsild 6826*, 15–17 Aug. 1933 (GH)). White bars = 100 μm.









FIGURES 80–87. Seeds of northeastern North American species of *Saxifraga*. 80, Sect. SAXIFRAGA: *S. cespitosa* (Canada, Québec, Richmond Gulf, e. coast Hudson Bay, *Abbe et al. 3601*, 1 Aug. 1939 (GH)). 81, Sect. TRACHYPHYLLUM Gaudin: *S. tricuspidata* (Canada, Québec, Port Harrison, e. coast Hudson Bay, *Malte 12089*, 18–20 Aug. 1928 (GH)). 82–85, Sect. XANTHIZOON Griseb., *S. aizoides*: 82, fossil seed from Columbia Bridge site, cell walls obscured by mineral particles; 83, 84, two seeds from same capsule, herbarium specimen (Canada, Newfoundland, Bonne Bay region, *Fernald & Wiegand 3521*, 27 Aug. 1910 (GH)); 85, less mature seed from herbarium specimen showing broader, less contracted papillae than those in Figures 83, 84 (Canada, Québec, Bonaventure

plants, and a few species that now show an eastern-western North American pattern of disjunction. The disjunct eastern populations were at one time thought to indicate the existence of unglaciated refugia in the area adjacent to the Gulf of St. Lawrence, but the fossils show that some species with this pattern grew on recently deglaciated surfaces south of their present area of occurrence. The distribution of such plants may have been much wider in late glacial time than is now the case, although the suggestion that western plants may have migrated eastward during the time of general ice recession must await confirmation from more paleobotanical evidence. Some of them may have had a long history of occurrence in the East.

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APPENDIX A. Percentages of pollen and spores from the Columbia Bridge site not included in pollen diagram.

Tsuga: 0.3% (1.00–1.05 m.), 0.2% (1.10–1.15 m.), 0.5% (3.49–3.59 m.).
Larix: 0.2% (1.55–1.60 m.).
Populus: 0.3% (0.40–0.45 m.), 1.1% (0.90–0.95 m.), 0.3% (1.10–1.15 m.), 0.2% (1.20–1.25 m.), 0.2% (1.30–1.35 m.), 0.2% (1.50–1.55 m.), 0.2% (3.49–3.59 m.).
cf. *Engelhardtia*: 0.5% (0.50–0.55 m.), 0.2% (0.60–0.65 m.), 0.7% (0.70–0.75 m.), 0.6% (0.80–0.85 m.), 1.8% (1.10–1.15 m.), 1.1% (1.55–1.60 m.).
cf. *Platycarya*: 1.2% (0.80–0.85 m.), 0.2% (1.35–1.40 m.).
Juglans: 0.7% (0.40–0.45 m.), 0.3% (0.60–0.65 m.), 0.2% (1.20–1.25 m.).
Fagus: 0.3% (0.30–0.35 m.), 0.2% (1.20–1.25 m.), 0.2% (1.55–1.60 m.).
Castanea: 0.5% (3.49–3.59 m.).
Ulmus: 0.5% (0.20–0.25 m.), 0.3% (0.40–0.45 m.), 0.6% (0.80–0.85 m.), 0.3% (0.90–0.95 m.), 0.2% (1.10–1.15 m.), 0.4% (1.20–1.25 m.), 0.4% (1.50–1.55 m.), 0.2% (1.55–1.60 m.), 0.5% (3.49–3.59 m.).
Ericaceae: 0.2% (0.20–0.25 m.), 0.3% (0.30–0.35 m.), 0.4% (0.40–0.45 m.), 0.3% (0.90–0.95 m.), 0.3% (1.00–1.05 m.), 0.6% (1.20–1.25 m.), 0.2% 1.30–1.35 m.), 0.2% (1.50–1.55 m.).
cf. *Dryas Drummondii*: 0.3% (0.10–0.15 m.), 0.2% (0.30–0.35 m.).
Other Rosaceae: 0.2% (3.49–3.59 m.).
Chenopodiaceae-Amaranthaceae: 0.5% (0.30–0.35 m.), 0.3% (0.60–0.65 m.), 0.6% (0.80–0.85 m.), 0.2% (1.30–1.35 m.), 0.2% (1.50–1.55 m.).
Nymphaea: 0.3% (3.49–3.59 m.).
Typha latifolia: 0.4% (0.30–0.35 m.), 0.2% (1.55–1.60 m.).
Sparganium: 0.2% (0.30–0.35 m.), 0.3% (0.40–0.45 m.).
Botrychium: 0.2% (0.40–0.45 m.), 0.1% (1.10–1.15 m.), 0.3% (1.50–1.55 m.), 0.3% (1.55–1.60 m.), 0.2% (3.49–3.59 m.).

APPENDIX B. Morphological notes on seeds and fruits.

Arenaria. Seeds of the 20 native sandworts listed by Fernald (1950; only northern species examined) and Boivin (1966–67) differ in size (largest, *A. peploides* L., to 4 mm. long; smallest, *A. rubella* (Wahlenb.) Sm., ca. 0.5 mm. long); in shape (from side, more or less elliptic in most, angular in *A. groenlandica* (Retz.) Sprengel); in having (*A. capillaris* Poiret *s. l.*, *A. laricifolia* L., *A. marcescens* Fern.) or lacking a beak near the hilum; in having (*A. lateriflora* L., *A. macrophylla* Hooker) or lacking a strophiole; in the presence (*A. macro-*

carpa Pursh) of a crest of enlarged finger-like cells; and in cellular configuration of the seed coat (black and shiny, adjoining cell walls just visible with the dissecting microscope (*A. lateriflora* L., *A. lanuginosa* (Michaux) Rohrb.) or not discernible (*A. macrophylla* Hooker), adjoining cell walls strongly undulate (*A. caroliniana* Walter), moderately undulate (*A. capillaris* Poiret; *A. dawsonensis* Britton, FIGURE 32; *A. humifusa* Wahlenb.; *A. patula* Michaux, FIGURE 36; *A. Rossii* R. Br., FIGURE 35; *A. rubella*; *A. stricta* Michaux, FIGURE 37), weakly undulate (*A. groenlandica* (Retz.) Sprengel), or adjoining walls mostly not discernible but seed coat brown rather than black and shiny (*A. sajanensis* Willd.)). Seed-coat cells can be seen under a dissecting microscope at high magnification, but scanning electron microscopy is necessary for appraisal of detail.

Saxifraga. Of the sixteen species of *Saxifraga* attributed to northeastern North America by Fernald (1950), Polunin (1940), and Scoggan (1950), we have evaluated external seed morphology by scanning electron microscopy in all but *S. cernua* L., *S. gaspensis* Fern., and *S. Geum* L., for which seeds were not available. Seeds of the species studied are ellipsoid or oblong, and when dry (usually also when wet) have one, or sometimes two, prominent longitudinal folds. Variation is also discernible in size (smallest, ca. 0.5 mm., *S. virginiensis* Michaux, FIGURE 74; *S. rivularis* L., FIGURE 79), shape, and length to width ratios. Configuration of the mature seed coat seems to differ consistently from species to species. Seed coat differences can reflect maturity (cf. seeds from ripe capsule, FIGURES 83, 84, vs. immature seed, FIGURE 85); thus, the most meaningful comparisons are made between fully mature seeds. Outer walls of seed coat cells can be strongly bulging (*S. hieracifolia* Waldst. & Kit., FIGURE 72; *S. stellaris* L., FIGURE 76; *S. virginiensis* Michaux, FIGURE 74; *S. pensylvanica* L., FIGURE 75), weakly bulging (*S. nivalis* L., FIGURE 73; *S. Hirculus* L., FIGURE 77), or elaborated into long and spinelike (*S. aizoides* L., FIGURES 83, 84) or short, sharply defined (*S. Aizoon* L., FIGURE 86) papillae. Papillae or bulging cells are often arranged in longitudinal rows that can be seen with a dissecting microscope. Outer walls of seed coat cells can also be pluripapillose (*S. cespitosa* L., FIGURE 80; *S. flagellaris* Willd. ex Sternb., FIGURE 78; *S. oppositifolia* L., FIGURE 87; *S. rivularis* L., FIGURE 79; *S. tricuspidata* Rottb., FIGURE 81), although anticlinal cell walls may not be fully apparent. Kaplan (1976) has drawn attention to morphological differences in seed coats of certain European alpine species of *Saxifraga*, as has Conolly (1976).

Potentilla. Achenes of *Potentilla*, *Fragaria*, and *Sibbaldia* are of simiar size and general appearance. However, in each genus the achene apex differs in the following ways (Godwin, 1975): central and obtuse (*Sibbaldia*, FIGURE 28); blunt and ventrally inclined (*Potentilla*, FIGURE 29); pointed and strongly inclined (somewhat hooked) toward the ventral suture (*Fragaria*). Achenes of certain species of *Potentilla* are sufficiently distinct to allow identification of well-preserved fossil material, providing accurately determined comparative specimens are at hand. Species (notes pertain to native northern taxa in Fernald (1950) and to all species in Polunin (1940) and Scoggan (1950)) differ in having achenes densely hairy (*P. fruticosa* L., *P. tridentata* Aiton); the achene surface smooth or finely to coarsely ridged (*P. anglica* Laich., *P. canadensis* L., *P. Crantzii* (Crantz) G. Beck, *P. effusa* Douglas, *P. erecta* (L.) Hampe, *P. millegrana* Engelm., *P. nivea* L., *P. norvegica* L., *P. pectinata* Raf., *P. pensylvanica* L., *P. pulchella* R. Br., *P. tridentata* Aiton, and *P. rivalis* Nutt.); the dorsal su-

ture prominent (*P. anserina* L., *P. Egedei* var. *groenlandica* (Tratt.) Polunin); the ventral suture enlarged and ridged (*P. Nicolletii* (S. Watson) Sheldon, *P. paradoxa* Nutt., *P. rivalis* Nutt.); the ventral suture long in relation to total achene length (*P. pensylvanica* L.); and in the size of the achene (e.g., smallest (0.75 mm. high, 0.5 mm. wide), *P. millegrana* Engelm., *P. pentandra* Engelm.). Achenes of *P. arguta* Pursh are similar to those of *Fragaria* in having a short, apical, ventrally oriented, beaklike projection.

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THE CONVOLVULACEAE OF THE LESSER ANTILLES

Dulcie A. Powell

This study of the Convolvulaceae comprises 58 species in 10 genera native to or naturalized in the islands of the Lesser Antilles, extending from Anguilla in the north to Grenada in the south. Specimens are cited only in cases of new records for the area and for a new species, *Evolvulus antillanus*. Descriptions have all been prepared from actual specimens, except in the few instances where none was available, and then a note is made to that effect.

Common ornamentals are included in the Keys, and a short section on cultivated taxa is given at the end.

When the actual date of a publication is known to be different from that on the title page, the correct date is given in square brackets.

CONVOLVULACEAE

Annual or perennial, twining or prostrate plants, erect shrubs, or occasionally trees. Leaves alternate, rarely stipulate, simple, entire or lobed, or palmately compound. Flowers axillary, solitary or in cymes, bracteate; aestivation induplicate, exposed portions of bud thickened and forming a star in open flower, imbricate in *Cuscuta*; sepals (4 or) 5, usually free, imbricate, equal or unequal, persistent; petals (4 or) 5, joined, limb entire or lobed, generally actinomorphic, usually showy; stamens alternating with corolla lobes, inserted near the base of the corolla tube (except in *Cuscuta*), usually flattened and bearing glandular hairs at their bases; ovary often surrounded by disc, superior, with 1 to 4 locules, usually 2, the ovules axile, erect, the style(s) 1 or 2. Capsule dehiscing by valves, circumscissile, splitting irregularly, or indehiscent; seeds usually 4, glabrous or hairy.

Key to the Genera of Convolvulaceae in the Lesser Antilles

1. Plants parasitic; stem yellow or orange; leaves reduced to scales. . . . . 1. *Cuscuta*.
1. Plants autotrophic, with green leaves.
   2. Herb or undershrub, not twining; styles 2. . . . . 2. *Evolvulus*.
   2. Shrub or usually a twining or trailing vine; style 1.
      3. Flowers small and numerous, borne in large, creamy white panicles; a cultivated woody climber. . . . . *Porana paniculata* Roxb.
      3. Flowers not very small, or if small, not borne in large panicles.
         4. Stems and leaves bearing branched trichomes, especially when young.
            5. Stigmas filiform. . . . . 3. *Convolvulus*.
            5. Stigmas not filiform. . . . . 4. *Jacquemontia*.
         4. Plants with simple trichomes or glabrous.
            6. Pollen spiny; corolla not bright yellow in species known (see *Ipomoea* no. 17).

7. Fruits ellipsoid, circumscissile, mostly 1-seeded; flowers white with dark centers, borne in clusters. . . 10. *Turbina*.
7. Fruits globose or subglobose, not circumscissile, seeds more than 1; flowers if white not borne in clusters.
8. Fruits valvate. . . . . 8. *Ipomoea*.
8. Fruits indehiscent.
9. Sepals and lower leaf surfaces with glandular dots. . . . . 9. *Stictocardia*.
9. Sepals, lower leaf surfaces, and stems with dense, white tomentum; heavy vine; cultivated. . . . . *Argyreia nervosa* (Burman f.) Bojer.

6. Pollen smooth; flowers frequently yellow.
10. Leaves simple, entire, narrowly elliptic. . . . . 5. *Aniseia*.
10. Leaves palmately divided or lobed, or broadly ovate.
11. Stems and peduncles often winged; exocarp separating as an operculum. . . . . 7. *Operculina*.
11. Stems and peduncles wingless (except occasionally in *M. umbellata*); capsule thin walled, with no operculum. . . . . 6. *Merremia*.

1. Cuscuta Linnaeus, Sp. Pl. 1: 124. 1753.

Total parasites, herbaceous, twining, attached to host by haustoria; stems orange or yellow, shining-smooth, brittle, containing clear latex. Leaves reduced to a few scales. Flowers small, white or cream, in crowded cymes; bracts present; perianth pentamerous in West Indian species; sepals united, free above; petals united, free above; stamens inserted on rim of corolla tube, with a fimbriate scale borne below each one; ovary bilocular, each cell containing 2 ovules, the styles 2 (in West Indian species), with capitate stigmas. Fruit a thin-walled capsule, sometimes circumscissile; seeds (1–)4.

LECTOTYPE SPECIES: *Cuscuta europaea* L.

KEY TO THE SPECIES OF CUSCUTA

1. Capsule not opening by circumscission, the greater part exposed at maturity.
2. Flowers wider than long, the sepal lobes rounded, overlapping at base. . . . . 3. *C. campestris*.
2. Flowers longer than wide, the sepal lobes acute, not overlapping. . . . . 5. *C. indecora*.
1. Capsule opening by circumscission, the greater part covered at maturity.
3. Stems coarse, growing mostly on shrubs; calyx and corolla lobes much shorter than the tubes.
4. Flowers 3–4 mm. long; capsule usually 2-seeded. . . . . 4. *C. globulosa*.
4. Flowers 2 mm. long; capsule usually 1-seeded. . . . . 1. *C. americana*.
3. Stems slender, growing mostly on herbs; calyx and corolla lobes about equal to, or longer than, the tubes.
5. Calyx and corolla lobes with irregular margins, rounded, with a horn-like projection at the apex. . . . . 2. *C. boldinghii*.
5. Calyx and corolla lobes entire, acute. . . . . 6. *C. umbellata*.

1. **Cuscuta americana** L. Sp. Pl. 1: 124. 1753.

Cuscuta surinamensis Schilling, Descr. Pl. Leprae, 60, 200. *pl. 2*. 1778.
Cuscuta graveolens H.B.K. Nov. Gen. Sp. 3: 122 (96 in folio ed.). 1818 [1819].
Nemepis americana (L.) Raf. Fl. Tellur. 4: 91. 1838.
?*Nemepis prolifera* Raf. *ibid.*
?*Dactylepis brownei* Raf. *ibid.* 125.
?*Eronema robinsoni* Raf. *ibid.*
Cuscuta spectabilis Choisy, Mém. Soc. Hist. Nat. Genève 9: 283. *pl. 5, fig. 1.* 1842.
Cuscuta leiolepis Miq. Linnaea 18: 247. 1844.
Cuscuta congesta Bentham, Bot. Voy. Sulphur, 138. 1845.
Cuscuta campanulata Nutt. ex Engelmann, Trans. Acad. St. Louis 1: 482. 1859.
Cuscuta americana L. var. *congesta* Progel in Martius, Fl. Brasil. 7: 376. 1871.
Cuscuta americana L. var. *spectabilis* Progel in Martius, *ibid.* 377.

COMMON NAMES. Teigne, vermicelle (St. Barts); love vine (St. Martin, St. Eustatius, Saba); vermicelle, corde à violon, herbe z'amitié, herbe à z'amourelle, herbe à z'amourette (Guadeloupe); vermicelle, corde de violon, liane à cordon, liane sans fin, herbe à z'amourette (Martinique); love vine (Barbados).

Stems medium to coarse. Flowers sessile to subsessile, congested, about 2 mm. long, drying straw-brown to black; calyx about as long as the corolla tube, the sepals joined to form a deep, campanulate tube lobed only near the top, the lobes overlapping below, rounded at the apex; corolla lobes shorter than the tube, erect, obtuse; filaments very short; stigmas capitate, exserted. Capsule ovoid-globose, circumscissile, bearing the persistent withered corolla as a crown; seed usually 1.

GENERAL DISTRIBUTION. Tropical America; most common in the West Indies.

DISTRIBUTION IN LESSER ANTILLES. Anguilla, St. Martin, St. Barts, Saba, St. Eustatius, St. Kitts, Nevis, Antigua, Montserrat, Guadeloupe, Dominica, Martinique, Barbados, St. Vincent, Bequia, Carriacou, Ronde, Grenada.

2. **Cuscuta boldinghii** Urban, Repert. Sp. Nov. 16: 38. 1919.

Cuscuta partita Boldingh, Fl. Nederl. W.-Ind. Eil. 326. 1913, non Choisy, 1842.
Cuscuta ceratophora Yuncker, Illinois Biol. Monogr. 6: 118. *figs. 29, 72.* 1921.

Stems slender, bearing very compact, isolated clusters of sessile or subsessile flowers, turning somewhat black on drying. Flowers 3–4 mm. long; calyx equal to or longer than the corolla tube, sepals united only at the base; corolla lobes upright or slightly spreading, about equal to the corolla tube in length; petals and sepals slightly denticulate, rounded at the tops, with apical or subapical, hornlike projections; stigmas globose, the styles

sturdy, longer than the ovary. Capsule circumscissile, bearing the withered corolla on top.

GENERAL DISTRIBUTION. Mexico, Central America, West Indies.

DISTRIBUTION IN LESSER ANTILLES. Grenada.

3. **Cuscuta campestris** Yuncker, Mem. Torrey Bot. Club **18**: 138. 1932.

?*Cuscuta americana* Hooker, Fl. Bor.-Am. **2**: 77. 1840 [1837], non Linnaeus, 1753.

Cuscuta pentagona Engelmann var. *calycina* Engelmann, Am. Jour. Sci. Arts **45**: 76. 1843.

Cuscuta arvensis Engelmann in Gray, Man. Bot. 336. 1856, p. p., non Beyrich, 1838.

Cuscuta arvensis Engelmann var. *calycina* Engelmann, Trans. Acad. St. Louis **1**: 495. 1859.

?*Cuscuta arvensis* Engelmann var. *capsici* Degen & Linhart, Zeitschr. Pflanzenkrank. **17**: 269. 1908.

Cuscuta pentagona Engelmann var. *subulata* Yuncker, Am. Jour. Bot. **10**: 3. 1923, p. p.

COMMON NAMES. Liane z'amitié, liane vermicelle (Guadeloupe and Martinique).

Stems slender. Flowers pedicellate, borne in numerous small clusters, 2–3 mm. long, wider than long; calyx as long as corolla tube, the lobes rounded, overlapping at base; corolla lobes reflexed, acute, about as long as the tube or longer, sometimes verrucose on the outside; stamens and fimbriate scales pointing inward toward styles; intrastylar opening conspicuous; persistent calyx and corolla not enclosing the depressed-globose capsule.

GENERAL DISTRIBUTION. Cosmopolitan.

DISTRIBUTION IN LESSER ANTILLES. Guadeloupe, Marie Galante, Martinique. Where *Polygonum* occurs, it is a favorite host of this *Cuscuta*.

4. **Cuscuta globulosa** Bentham, Bot. Voy. Sulphur, 138. 1845, non Boissier, 1856.

Cuscuta americana L. var. *spectabilis* Yuncker, Illinois Biol. Monogr. **6**: 124. 1921, p. p.

COMMON NAMES. See *Cuscuta americana*.

Stems coarse. Flowers 3–4 mm. long, subsessile to shortly pedicellate, drying straw-yellow; calyx about as long as the corolla tube, the sepals joined to form a deep, campanulate tube, lobed at the top, the lobes rounded at the apex, overlapping at the base; corolla lobes erect, obtuse, shorter than the corolla tube; filaments very short; stigmas capitate, exserted. Capsule depressed-globose, circumscissile, bearing the persistent withered corolla as a crown; seeds usually 2.

GENERAL DISTRIBUTION. Mexico, West Indies.

DISTRIBUTION IN LESSER ANTILLES. St. Barts (*fide* Questel), Montserrat, Martinique, St. Vincent.

Cuscuta globulosa is very closely related to *C. americana*. When dry, the lighter color of its larger and fewer flowers is in marked contrast to those of *C. americana*, as is the shape of the capsule, which varies with the number of seeds. However, intermediate forms are to be found that make the distinction questionable at the species level. The response of these species and intermediate forms to host plants might prove to be a very rewarding study.

Both species are robust and occasionally produce straight flowering shoots that do not twine and that bear no haustoria.

5. **Cuscuta indecora** Choisy, Mém. Soc. Hist. Nat. Genève 9: 278. *pl. 3, fig. 3.* 1842.

Cuscuta verrucosa Engelmann var. *hispidula* Engelmann, Am. Jour. Sci. Arts **43:** 341. 1842.
Cuscuta hispidula (Engelmann) Engelmann, *ibid.* **45:** 75. 1843.
Cuscuta neuropetala Engelmann var. *minor* Engelmann, Boston Jour. Nat. Hist. **5:** 223. 1845.
Cuscuta porphyrostigma Engelmann, *ibid.*, in synon.
Cuscuta decora Engelmann, Trans. Acad. St. Louis **1:** 501. 1859.
Cuscuta decora var. *indecora* Engelmann, *ibid.* 502.
Cuscuta parviflora Engelmann var. *vestita* Progel in Martius, Fl. Brasil. **7:** 386. 1871.
Epithymum indecorum (Choisy) Nieuwland & Lunell, Am. Midl. Nat. **4:** 511. 1916.
Cuscuta indecora Choisy var. *hispidula* (Engelmann) Yuncker, Illinois Biol. Monogr. **6:** 148. 1921.

Stems slender. Inflorescence papillose, usually elongate, with several flowers; pedicels longer than flowers; calyx shorter than corolla tube, the lobes acute, not overlapping at the base; corolla about 3 mm. long, fleshy, the lobes blunt or acute, outspread and with incurved tips in mature flowers. Capsule globose, ca. 4 mm. across.

GENERAL DISTRIBUTION. Tropical America.

DISTRIBUTION IN LESSER ANTILLES. Barbados.

6. **Cuscuta umbellata** H.B.K. Nov. Gen. Sp. 3: 121 (95 in folio ed.). 1818 [1819].

Stems very slender. Flowers about 2 mm. long, pedicellate; calyx lobes acute, reaching up to the top of the corolla tube or longer; corolla lobes acute, about as long as the corolla tube or longer, reflexed, exposing the stamens and pistils; pistils longer than the ovary. Capsule depressed-globose, very fragile, somewhat exposed.

GENERAL DISTRIBUTION. Tropical America.

DISTRIBUTION IN LESSER ANTILLES. Saba (*fide* Boldingh), Antigua (*fide* Engelmann, Yuncker), Guadeloupe.

Boldingh (1909, 1913) reported this species from Saba, but Yuncker (Mem. Torrey Bot. Club 18: 237. 1932) did not mention having examined any West Indian specimen except a Wullschlaegel collection from Antigua, which he listed under *Cuscuta umbellata* var. *desertorum* Engelmann (Trans. Acad. St. Louis 1: 488. 1859) as Engelmann had done, observing that the specimen had immature capsules. According to Yuncker, the specimen had capsules that are more exposed and glandular and flowers that are broader than is typical for this variety. This raises the question as to whether Wullschlaegel's collection was in fact *C. campestris*.

It seems, therefore, that the distribution of *Cuscuta umbellata* in the Lesser Antilles is little known; the species does occur throughout the Greater Antilles.

Judging from material studied, *Cuscuta umbellata* is often very floriferous in the United States and Mexico, whereas West Indian material is much more vegetative, its relatively few flowers and fruits (with extremely thin calyx, corolla, and capsules) being obscured by its own stems and the foliage of the host plant. Members of the Portulacaceae and Amaranthaceae are the most frequent host plants for the species throughout its range. A striking resemblance between *C. umbellata* and the Argentinian *C. membranacea* Yuncker, added to their similar hosts, suggests that the latter species belongs here, the circumscission of its capsules being a factor of age.

2. **Evolvulus** Linnaeus, Sp. Pl. ed. 2. 1: 391. 1762.

Herbs, undershrubs, or shrubs, prostrate to erect, more or less hairy, the appressed trichomes essentially malpighiaceous, the patent hairs simple. Leaves small, simple, entire. Flowers axillary or terminal; bracts 2, at base of pedicel; sepals 5, free, equal or subequal; corolla rotate, funnel or salver shaped, small, usually blue or white, subentire or 5-lobed, the middle of each lobe hairy on the outside; stamens 5, filaments filiform, anthers ovate to linear; ovary glabrous or occasionally pilose, 1- or 2-celled, ovules 4, styles 2, each bifid, stigmas long, filiform. Capsule globose or ovoid, 4-valved, (1- to) 4-seeded; seeds smooth or minutely verrucose, glabrous.

LECTOTYPE SPECIES: *Evolvulus nummularius* L.

KEY TO THE SPECIES OF EVOLVULUS

1. Plants prostrate; leaves oblong to subrotund, base sometimes cordate or subcordate.
2. Stems anchored at nodes; hairs simple, not appressed; bracts borne in leaf axil; corolla distinctly lobed. ..... 5. *E. nummularius*.
2. Stems anchored by taproot, only occasionally rooting at nodes; hairs appressed; flowers pedicellate and pedunculate, not lobed. ..... 3. *E. convolvuloides*.

1. Plants usually ascending or upright; leaves ovate, elliptic, or linear, base never cordate or subcordate.
   3. Plants not sericeous.
      4. Leaves ovate; flowers ca. 1 cm. across; cultivated. . . . . *E. tenuis* Martius ex Choisy subsp. *longifolius* (Choisy) Ooststr.
      4. Leaves elliptic or linear; flowers less than 1 cm. across.
         5. Leaves elliptic, 2 or 3 times as long as wide; stems villose. . . . . 1. *E. alsinoides* var. *grisebachianus*.
         5. Leaves linear or elliptic, much longer than wide; stems strigose. . . . . 4. *E. filipes*.
   3. Plants sericeous, at least on undersides of leaves.
      6. Flowers pedunculate and pedicellate. . . . . 2. *E. antillanus*.
      6. Flowers without peduncles. . . . . 6. *E. sericeus*.

1. **Evolvulus alsinoides** (L.) L. var. **grisebachianus** Meissner in Martius, Fl. Brasil. 7: 344. 1869.

Evolvulus diffusus Chapman, Fl. So. U. S. 345. 1860.

Suberect to trailing herb, branching at ground level; stems villose. Leaves shortly petiolate, elliptic, up to 15 mm. long and 8 mm. wide, apex mucronate or abruptly acute, the hairs appressed, often denser on the lower surface. Peduncles filiform, longer than the subtending leaves, bearing 1 (to several) flowers; pedicels 3–5 mm. long; calyx villose, the sepals 2–3 mm. long, ovate-lanceolate, acuminate; corolla blue or lavender, ca. 5 mm. wide, rotate, lobed. Capsule ca. 3 mm. across, straw colored; locule 1, with fragmentary septum; seeds 4.

General distribution. Tropical America.

Distribution in Lesser Antilles. St. Martin, Barbados.

2. **Evolvulus antillanus** Powell, sp. nov. Figure 1, a.

Evolvulus argyreus sensu auct., non Choisy, 1837; Ooststr. Monogr. Gen. *Evolvulus*, 80. 1934, p. p., excl. type.

Common names. Lin, lin bâtard (Martinique).

Herbae. Caules pauci vel multi, parvi et prostrati vel suberecti et trahentes usque 50 cm. longi, tenaces, sericei, vetustiores glabrescentes. Folia conferta, duplo longiora quam lata, fulvo-sericea in plantis prostratis, vel in plantis suberectis non conferta, 5-plo longiora quam lata, cinereo-sericea, breviter petiolata (petiolo trichomis obscuro), apice acuta, 5–12 mm. longa, ± 2 mm. lata, anguste oblongo-elliptica vel late elliptica, utrinque sericea, sed interdum in plantis majoribus supra glabrescentia; costa subtus prominente. Flores axillares, pedunculati, plerumque solitarii; pedunculus sericeus, folio subtento brevior vel longior; bracteae 2, aciculares, 1–2 mm. longae, apice pedunculi persistentes; pedicellus 3–7 mm. longus, sericeus; sepala 5, sericea, imbricata, ca. 3 mm. longa, duo exteriora lanceolata, acuta, tres interiora ovata, apice acuta, in partibus inferioribus inclusis margine scarioso, interdum puncta pellucida visa; co-

FIGURE 1. Lower portion of corolla tube opened and spread to show stamens and outgrowths, × 12: a, *Evolvulus antillanus*; b, *Evolvulus argyreus*.

rolla rotata cremeo-alba vel azurea, a basi ad marginem 5–6.5 mm. longa, extus sericea ad plicas; stamina paulo super basin corollae inserta; filamentum ± 2 mm. longum, anthera filamento 2-plo brevior plerumque torta; pollinis grana laevia; 5 cuspes breves infra corollae tubum inter filamentorum bases et eisdem alternantes triangulares sursum et introrsum projectae (interdum junctae) cucullum tholiformem super ovarium facientes; styli 2, filiformes superne in ramos longos filiformes 2 divisi; ovarium 1-loculare vel incomplete 2-loculare, ovula 4. Fructus glaber, globosus, stramineus, capsularis 4-valvatus, 2–3 mm. diametro; semina 4 vel minus, brunnescentia, glabra.

Prostrate or suberect herb; stems few to many, sericeous to glabrescent with age. Leaves 5–12 mm. long, ca. 2 mm. wide, narrowly oblong, elliptic, or broad-elliptic, fulvous- to gray-sericeous, sometimes glabrescent on the upper surface in larger plants, midrib prominent on lower surface. Flowers usually solitary; peduncle shorter or longer than subtending leaf; pedicel 3–7 mm. long; sepals sericeous, ca. 3 mm. long; corolla about twice as long, white or blue, the tube with 5 short, triangular cusps between the bases of the filaments, alternating with them, projecting upward and inward (sometimes joining) over the ovary; ovary 1- or incompletely 2-celled, ovules 4. Capsule globose; seeds 4 or fewer.

SPECIMENS EXAMINED. (**St. Martin:** *Boldingh 3371* cited under *E. argyreus* is also cited under *E. sericeus* (Boldingh, 1909, p. 160)). **Antigua:** near English Harbour, *Rose, Fitch, & Russell 3356* (US, type). **Barbuda:** Lignum Vitae Trail, *Box 625* (GH, US). **Guadeloupe:** littoral madréporique, falaises, Pointe des Châteaux, *Stehlé 2810* (US); Côte sous le Vent, Baillif, *H. & M. Stehlé 5939* (US). **Martinique:** Ste. Anne, calcaires des pétrifications falaises littorales xérophiles, alt. 10 m., *H. Stehlé 2304* (US); pelouses xérophiles, Le Marin, sud de l'île sur sol parsemé de bois silicifiés, 30 m., *H. & M. Stehlé 3676* (GH, US); pelouses

xéro-héliophiles, Le Diamant, sud de l'île, alt. 40 m., *H. & M. Stehlé 3692* (US); pelouses xérophytiques littorales de sud, Anses d'Arlet, alt. 15 m., *H. & M. Stehlé 4382* (US); mornes salines, falaises madréporiques, alt. 24 m., *H. & M. Stehlé 6177* (A, US), *Hahn 1136* (US); environs de fort de Fort de France, *Hahn 1336* (GH). **St. Lucia:** volcanic sea-cliffs at Marquis Bay, 20–200 ft., *Proctor 17559* (A); sea cliffs, 50 ft., Port Dauphin, *Sturrock 499* (A). **Curaçao:** rocky hills, Wacao to Playa Grande, *Britton & Schafer 3037* (US).

Evolvulus antillanus occurs in Curaçao and probably also in neighboring Venezuela. In fact, *Curran & Haman 527* from northern Venezuela seems to belong to this species, but because the material at hand is sterile, the evidence is inconclusive.

Several flowers examined had incompletely fused ovaries, the four valves separating at the apex. This may have been partly due to pressing, but no fresh or preserved material has been available for study.

In his monograph of the genus *Evolvulus*, van Ooststroom (Meded. Bot. Mus. Utrecht **14**: 80–82. 1934) placed certain collections of West Indian material with some from South America in the species *E. argyreus* Choisy because, in his opinion, there was no distinct difference between the specimens. However, additional collections from the Lesser Antilles show that the specimens from this area are, in fact, distinct from the South American species, and we are here describing them as the new species *Evolvulus antillanus*.

Small plants of both species are remarkably alike with their crowded, fulvous, sericeous leaves. Larger plants show less similarity: the leaves of *Evolvulus argyreus* are twice as wide; the plant is more foliaceous and less wiry; the flowers are larger and of a deeper blue than those of *E. antillanus*. Material from St. Lucia is even more distinct, having gray indumentum and a more pronounced trailing habit. On the lower leaf surfaces of *E. antillanus*, unlike those of the other species, only the midrib is discernible. Near the base of the corolla tube, five triangular cusps arising at the same level as, and alternating with, the stamens, curve inward to form a dome-shaped hood over the ovary, whereas in *E. argyreus* (FIGURE 1, b) there are typically two narrow flaps produced on the corolla tube below the level of each stamen and converging at its base; these two flaps sometimes join tips to form a tooth opposite the stamen, and always reach up to the base of the stamen rather than beyond. They do not form a hood over the ovary. This condition (as in *E. argyreus*) has also been observed in *E. tenuis* Martius ex Choisy, in *E. arizonicus* A. Gray, in *E. incanus* Pers., and sometimes in *E. convolvuloides* (Willd. ex Schultes) Stearn. The habitats of the two species also differ: *E. argyreus* typically grows between 1000 and 3000 meters altitude in South America; *E. antillanus*, on dry West Indian coastland.

3. **Evolvulus convolvuloides** (Willd. ex Schultes) Stearn, Taxon **21**: 649. 1972.

Nama convolvuloides Willd. ex Schultes, Syst. Veg. **6**: 189. 1820.
Evolvulus nummularius sensu auct. non L. 1762.

Evolvulus hirsutus sensu auct. non Lam. 1789.
Evolvulus glaber Sprengel, Syst. Veg. 1: 862. 1824.
Evolvulus mucronatus Sw. ex Wikström, Sv. Vet.-Akad. Handl. 61. 1827.
Evolvulus glabriusculus Choisy, Mém. Soc. Hist. Nat. Genève 8: 78. 1837.
Majera coerulea Karsten ex Peter in Engler & Prantl, Nat. Pflanzenfam. 4(3a): 19. 1897.
Evolvulus karstenii Peter in Engler & Prantl, *ibid.*
Evolvulus campestris Brandegee, Univ. Calif. Publ. Bot. 6: 190. 1915.

COMMON NAME. Teigne (Guadeloupe).

Prostrate to trailing herb, arising from taproot, rarely rooting at the nodes, with appressed hairs or sometimes glabrescent. Leaves shortly petiolate; blade subrotund, oblong to obovate, 0.5–2.5 cm. long, 0.3–1.6 cm. wide, midrib and primary veins often prominent, upper surface glabrous or with few appressed hairs, lower surface with appressed hairs, the apex rounded or retuse (very occasionally somewhat acute), mucronate, the base rounded or subcordate. Peduncles shorter to longer than subtending leaves, usually 1-flowered; bracts 1–3 mm. long, linear, persistent; pedicels 2–4 mm. long; calyx pilose to glabrous, the sepals lanceolate, 2–4 mm. long, apex acute to acuminate; corolla pale blue or white, 8–10 mm. in diameter, pilose to glabrous on the outside, rotate, sometimes bearing 5 pairs of narrow flaps at the base within, each pair converging up to the base of a stamen; stamens attached ca. 1/6 height of corolla; ovary 1-celled, ovules 4. Capsule ovoid to globose, with a slightly pointed apex; seeds 4 or less.

GENERAL DISTRIBUTION. Tropical America.

DISTRIBUTION IN LESSER ANTILLES. Anguilla, St. Martin, St. Barts, St. Kitts (*fide* van Ooststroom), Antigua, Guadeloupe, La Désirade, Marie Galante, Martinique, St. Lucia, St. Vincent, Cannouan, Carriacou, Ronde, Mustique, Barbados (*fide* van Ooststroom), Grenada.

4. **Evolvulus filipes** Martius, Flora Beibl. 1841, Band 2, 100. 1841.

Evolvulus linifolius sensu auct. non L. 1762; Duss, Ann. Inst. Colon. Marseille 3: 442. 1897.
Evolvulus exilis Meissner in Martius, Fl. Brasil. 7: 342. *t. 123, fig. 1.* 1869.
Evolvulus saxifragus Martius var. *paraensis* Meissner in Martius, *ibid.* 343.
Evolvulus nanus Meissner in Martius, *ibid.* 346.
Evolvulus filipes Martius var. *exilis* (Meissner) Chodat & Hassler, Bull. Herb. Boiss. II. 5: 684. 1905.

COMMON NAME. Herbe grise (Martinique).

Semi-erect to decumbent herb, sparsely substrigose with appressed hairs; main stem frequently much branched, arising from a taproot. Leaves short petiolate to sessile, lanceolate to linear, up to 25 mm. long and 5 mm. broad, becoming smaller toward the top of the plant, midrib prominent beneath, very sparsely strigose to glabrous above, sparsely strigose

to glabrescent beneath, backward arm of each hair (on stem and leaf) very short or missing. Inflorescences sometimes branched; flower(s) 1 to several per peduncle; peduncle filiform, pilose, usually 2–2.5 cm. long and almost upright, considerably longer than the leaves; pedicels about as long as calyx; sepals sparsely pilose and ciliate, ca. 2 mm. long, ovate, acute at apex, green in flower, slightly accrescent and turning brown in fruit; corolla very small, slightly longer than calyx, blue; ovary 2-celled, ovules 4. Capsule globose, 2 mm. in diameter; seeds 4.

GENERAL DISTRIBUTION. Mexico to South America, Jamaica, Lesser Antilles.

DISTRIBUTION IN LESSER ANTILLES. Martinique, Grenada.

5. **Evolvulus nummularius** (L.) L. Sp. Pl. ed. 2. 391. 1762.

Convolvulus nummularius L. Sp. Pl. 157. 1753.
Evolvulus veronicaefolius H.B.K. Nov. Gen. Sp. **3:** 117 (92 in folio ed.). *t. 215.* 1818 [1819].
Evolvulus reniformis Salzm. ex Choisy, Mém. Soc. Hist. Nat. Genève **8:** 72. 1837, in synon.
Evolvulus domingensis Sprengel ex Choisy, *ibid.*, in synon.
Evolvulus capreolatus Martius ex Choisy, DC. Prodr. **9:** 445. 1845, in synon.
Evolvulus dichondroides Oliver, Trans. Linn. Soc. **29:** 117. *t. 78B.* 1875.
?*Evolvulus repens* Parodi, Contr. Fl. Paraguay, Fasc. **1:** 29. 1877.
Evolvulus nummularius (L.) L. var. *grandifolia* Hoehne, Anex. Mem. Inst. Butantan Bot. **1**(6): 39. 1922.

COMMON NAMES. Véronique (Guadeloupe); teigne, ti teigne, petite véronique, véronique bord de mer (Martinique).

Prostrate herb rooting at nodes; stems pilose with patent, crooked hairs. Leaves petiolate, petiole channeled above; blade oblong-elliptic to subrotund, 5–15 mm. long, 4–14 mm. wide, usually with pellucid dots, midrib and primary veins (3 to 5 pairs) prominent on the lower surface, with or without hairs, usually glabrous on the upper surface, hairs more numerous on midrib and veins on the lower surface, apex rounded to retuse, base rounded to cordate. Flowers solitary, lacking peduncle, sometimes crowded on short flowering branches; bracts 2 in leaf axil at base of pedicel; pedicel 2–4 mm. long, lengthening and becoming reflexed in fruit; calyx green, often tinged purple, the sepals ca. 3 mm. long, equal, ovate to oblong with acute tip, with pellucid dots and conspicuous midrib; corolla white, occasionally pale violet, 8–10 mm. in diameter, distinctly 5-lobed, sparsely pilose on outer surface of star; ovary 1-celled, ovules 4. Capsules brown or purple, 4-valved but splitting irregularly, conical to globose, slightly beaked; seeds 1 or 2, shape of fruit varying with number of seeds.

GENERAL DISTRIBUTION. Mexico to northern Argentina, West Indies, tropical Africa, Madagascar, India.

DISTRIBUTION IN LESSER ANTILLES. St. Barts, Antigua, Guadeloupe,

Îles des Saintes, Marie Galante, Désirade, Dominica, Martinique, St. Lucia, Barbados, Carriacou, Grenada.

6. **Evolvulus sericeus** Swartz, Prodr. 55. 1788 (as *Evolvolus*).

Evolvulus sericeus Sw. var. β Desr. in Lam. Encyl. Méth. Bot. **3:** 538. 1792.
Convolvulus proliferus Vahl, Eclog. **1:** 18. 1796 [1797].
Evolvulus sericeus Sw. var. *Commersoni* Pers. Syn. Pl. **1:** 288. 1805.
Evolvulus angustissimus H.B.K. Nov. Gen. Sp. **3:** 116 (91 in folio ed.). 1818 [1819].
Evolvulus Commersoni (Pers.) Schultes, Syst. Veg. **6:** 197. 1820.
Evolvulus virgatus Willd. ex Schultes, *ibid.* 198.
Convolvulus Commersonii Desr. ex Steudel, Nomencl. Bot. ed. 2. **1:** 408, 621. 1840, in synon.
?*Evolvulus brevipedicellatus* Klotzsch in Schomb. Versuch Fauna Fl. Brit. Guiana, 1153. 1848, *nomen nudum.*
Evolvulus sericeus Sw. var. *latior* Meissner in Martius, Fl. Brasil. **7:** 353. 1869.
Evolvulus anomalus Meissner in Martius, *ibid.*
Evolvulus alsinoides L. var. *sericeus* (Sw.) Kuntze, Rev. Gen. Pl. **2:** 441. 1891.
Evolvulus sericeus Sw. forma *glabrata* Chodat & Hassler, Bull. Herb. Boiss. II. **5:** 685. 1905.
Evolvulus sericeus Sw. var. *angustifolius* Hoehne, Anex. Mem. Inst. Butantan Bot. **1**(6): 42. 1922.
Evolvulus sericeus Sw. var. *loefgrenii* Hoehne, *ibid.*

COMMON NAME. Herbe argentée (Guadeloupe).

Low, wiry herb; stems few or several, upright or ascending, sericeous, 10–30 cm. long. Leaves linear or lanceolate, acute at apex, 5–30 mm. long, 3–8 mm. wide, sericeous on lower surface, usually glabrous above, midrib depressed above and prominent beneath, with one pair of primary veins in wider leaves. Flowers solitary or occasionally few; peduncle lacking; bracts in leaf axil; pedicel short; sepals equal, ovate, acuminate, usually with spreading tips, 3–5 mm. long, ciliate, sericeous outside and sometimes inside above; corolla white, rotate or wide funnel shaped, 7–12 mm. wide. Capsule globose, bilocular; seeds 4.

GENERAL DISTRIBUTION. Southern United States to Argentina, West Indies.

DISTRIBUTION IN LESSER ANTILLES. Anguilla, St. Martin, St. Barts, St. Eustatius, Antigua, Guadeloupe, Désirade, Dominica.

3. **Convolvulus** L. Sp. Pl. 153. 1753; Gen. Pl. ed. 5. 76. 1754.

Herbs or shrubs, twining, prostrate or erect, glabrous or hairy, the hairs simple or branched. Leaves usually entire. Flowers solitary, in axillary cymes or in terminal heads; bracts variable, persistent; sepals persistent; corolla funnel shaped or campanulate, white, blue, pink, purple, or yellow; stamens included, pollen smooth; style 1, stigmas 2, filiform, ovary 2-celled, ovules 4. Capsule 4- or 8-valved; seeds 4 or fewer, 3-angled with 2 sides flat and 1 convex, glabrous or pubescent, often rough.

LECTOTYPE SPECIES: *Convolvulus arvensis* L.

Convolvulus nodiflorus Desr. in Lam. Encycl. Méth. Bot. 3: 557. 1792.

Ipomoea verticillata sensu L. Plantarum Jamaicensium Pugillus, 9. Nov. 1759, non L. Syst. Nat. ed. 10. 924. May–June, 1759.
Jacquemontia nodiflora (Desr.) G. Don, Gen. Syst. 4: 283. 1838 [1837?].
Jacquemontia simulata House, Bull. Torrey Bot. Club 33: 314. 1906.

Woody vine, pubescent with short, 3-armed hairs or glabrescent. Petiole up to 2.5 cm., usually ± 1 cm. long; blades entire, ovate, up to 6 cm. long, pubescent or glabrate, the base cordate, subcordate, truncate, or very slightly cuneate (Grenada specimens), with the sides tending to be subequal, the apex usually acute or acuminate, mucronate. Inflorescences pedunculate, peduncles usually shorter than subtending petioles; flowers many and crowded to few or occasionally solitary; bracts small, pubescent, persistent; pedicel(s) less pubescent or glabrous, less than 1 cm. long; sepals rounded or obtuse at apex, scarious on edges, 2–3 mm. long, glabrous or pubescent; corolla white, wide funnel shaped, flaring from the base, slightly or distinctly lobed, 11–14 mm. long; stamens included; stigma bilobed, filiform, exserted when mature. Capsule ovoid, 3–4 mm. high, splitting into 4 and then into 8 valves; seeds 4 or fewer, brown, glabrous, ruminate, narrowly winged on the margins.

GENERAL DISTRIBUTION. West Indies, South America.

DISTRIBUTION IN LESSER ANTILLES. St. Martin, St. Barts, Guadeloupe, Martinique, St. Lucia, Barbados, St. Vincent, Cannouan, Grenada.

4. **Jacquemontia** Choisy, Mém. Soc. Hist. Nat. Genève 6: 476. 1834.

Perennial or annual vines, prostrate herbs, or shrubs; stems usually somewhat woody, with many branches, pubescent, with trichomes typically branched. Leaves simple, often bearing minute glandular dots. Peduncles usually longer than the subtending petioles; calyx variable; corolla blue, lavender, white, or occasionally reddish, entire or lobed, with convolvulaceous star prominent; stamens and pistil often exposed; pollen smooth; style 1; stigmas 2, not filiform. Capsule bilocular, valves 8 or fewer (tardily dehiscent?), brown outside, lighter inside and shining, the septum dark brown, opaque, shining, slightly uneven; seeds 4, glabrous, verrucose or ruminate, minutely areolate, often winged on the margins, with 3 sides, 2 flat and 1 convex.

TYPE SPECIES: *Jacquemontia azurea* (Desr.) Choisy.

KEY TO THE SPECIES OF JACQUEMONTIA

1. Prostrate herb with strigose, 2-armed trichomes and fleshy, obcordate leaves. ..... 4. *J. ovalifolia* subsp. *obcordata*.
1. Climbing or shrubby plants with trichomes and leaves otherwise.
   2. Flowers borne in hirsute, headlike cymes. ..... 7. *J. tamnifolia*.
   2. Flowers otherwise.

3. Leaves cordate or broadly ovate; corolla not deeply lobed.
   4. Inflorescence very lax; flowers tubular, red-purple. ..... 6. *J. solanifolia.*
   4. Inflorescence not very lax; flowers funnel shaped, blue.
      5. Leaves and stems velvety. ..... 2. *J. cumanensis.*
      5. Leaves and stems not velvety. ..... 5. *J. pentantha.*
3. Leaves not broadly ovate or cordate; corolla deeply lobed.
   6. Inflorescence sessile or on a very short peduncle. ..... 8. *J. verticillata.*
   6. Inflorescence pedunculate.
      7. Leaves thick, often roundish; flowers solitary or few, on short peduncles. ..... 1. *J. cayensis.*
      7. Leaves not very thick, often linear or oblong; flowers solitary to several, in lax cymes. ..... 3. *J. havanensis.*

1. **Jacquemontia cayensis** Britton in Britton & Millspaugh, Fl. Bahamas, 349. 1920.

Scrambling shrub or woody vine with many branches; stems, petioles, peduncles, and pedicels pubescent, often hoary, the hairs very short and with several arms. Petioles usually 5 mm. or less; blades elliptic, obovate, oblong, or orbicular, rarely exceeding 3 cm. in length, with glandular dots on both surfaces and sometimes also lines on the lower surface, glabrous, sparsely pubescent, or tomentose, the apex retuse or blunt, usually mucronate, the base cuneate or rounded, the margin entire, often tinged reddish brown. Peduncles shorter or longer than subtending petioles; flowers solitary or few; bracts minute; pedicel(s) ridged, ca. 5 mm. long; sepals subequal, 2–3 mm. long, glabrous or pubescent, especially at the apex; corolla white, deeply 5-lobed, ca. 1 cm. long; stamens and pistil well exserted; stigmas kidney shaped. Capsule conical, ca. 4 mm. high, 8-valved; seeds 4, narrowly winged on 3 margins and sometimes around the hilum.

GENERAL DISTRIBUTION. West Indies.

DISTRIBUTION IN LESSER ANTILLES. Anguilla, St. Barts, Barbuda, Antigua.

Because *Jacquemontia cayensis* can be distinguished from the very similar and variable *J. havanensis* only by the degree of coarseness of its stems, the thickness of its leaves, and the size of its inflorescence, it seems questionable that the two species should be maintained as distinct.

2. **Jacquemontia cumanensis** (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 441 1891.

Convolvulus cumanensis H.B.K. Nov. Gen. Sp. 3: 99 (77 in folio ed.). 1818 [1819].
Convolvulus ferrugineus Vahl, Eclog. 1: 17. 1796 [1797], non *Jacquemontia ferruginea* Choisy, 1837.
Ipomoea ferruginea (Vahl) R. & S. Syst. Veg. 4: 240. 1819.
Ipomoea cumanensis (H.B.K.) G. Don, Gen. Syst. 4: 273. 1838 [1837?].

Woody vine with many branches, pubescent on all parts except the corolla and the inner parts of the flower, with trichomes 3-armed, overlapping. Petioles up to 1.5 cm.; blades velvety, ovate, midrib up to 4 cm. in length, cordate or truncate at base, slightly retuse to acute at apex and usually mucronate, with margins entire or somewhat repand and undulate. Peduncles usually exceeding subtending leaves, bearing a compact cyme of few to several flowers; bracts small, lanceolate, with fewer hairs on the upper surface; pedicels very short; sepals very unequal, the outer 3 clasping the flower, hairier on the outer surfaces, the 2 outermost about as long as wide, 6–8 mm., ovate, acute, the others decreasing in size, the innermost smallest, lanceolate, acuminate; corolla blue, funnel shaped, scarcely lobed, the petals mucronate, 12–16 mm. long; stamens unequal; stigmas kidney shaped. Capsule enveloped by the calyx, ovoid, 4–5 mm. long, straw colored, 8-valved; seeds 4, cream or brown, wingless or rarely with a trace of a wing.

GENERAL DISTRIBUTION. Puerto Rico, Virgin Islands, Netherlands West Indies, Venezuela.

DISTRIBUTION IN LESSER ANTILLES. St. Martin.

3. **Jacquemontia havanensis** (Jacq.) Urban, Symb. Antill. 3: 342. 1902.

Convolvulus havanensis Jacq. Obs. Bot. 2: 25. *t. 45, fig. 3.* 1767.
Convolvulus jamaicensis Jacq. *ibid.* 3: 6. 1768.
Convolvulus ruderarius H.B.K. Nov. Gen. Sp. 3: 96 (75 in folio ed.). 1818 [1819].
Convolvulus frondosus Willd. ex R. & S. Syst. Veg. 4: 303. 1819.
Ipomoea ruderaria (H.B.K.) G. Don, Gen. Syst. 4: 267. 1838 [1837?].
Convolvulus garberi Chapman, Bot. Gaz. 3: 11. 1878.
Convolvulus obtusifolius Sessé & Moçiño, La Naturaleza, ser. 2. 2: (Appendix, Fl. Mex.) 35. 1892 (as *Conuoluulus*).
Jacquemontia ruderaria (H.B.K.) Hallier f. in Solereder, Syst. Anat. Dicot. 641. 1899.

Woody climber with many branches, sparsely to densely pubescent with very short, stellate hairs. Leaves variable; petiole short; blade somewhat coriaceous, ovate, oblong, or linear, up to 5 cm. long, veins depressed above, surface often covered with microscopic glandular dots and sometimes lines, fewer hairs on larger (ovate) leaves, cuneate or rounded at base, rounded, acute or retuse, mucronate at apex, the margins entire, somewhat thickened and revolute in dry material. Peduncles longer than subtending petioles; flowers numerous to few, occasionally solitary; bracts reduced to scales; pedicel filiform; sepals 2–3 mm. long, unequal or subequal, rounded to acute at the apex, usually slightly mucronate, glabrous or with a few hairs especially at the apex, scarious on the edges; corolla white or pale rose-purple, ca. 1 cm. long, deeply lobed, rotate; stamens and pistil well exserted; stigmas kidney shaped. Capsule conical, ca. 5

mm. tall, brown, 8-valved; seeds 4, brown, winged on the 2 outer edges or on all 3 edges and around the hilum.

GENERAL DISTRIBUTION. Florida, Mexico, British Honduras, West Indies.

DISTRIBUTION IN LESSER ANTILLES. Barbuda, southwestern part of island, south of lagoon, *Smith 10463* (A, US); near River Landing, *Box 659* (US).

4. **Jacquemontia ovalifolia** (Vahl ex West) Hallier f. subsp. **obcordata** (Millspaugh) Robertson, Ann. Missouri Bot. Gard. **61**: 508. 1974.

Convolvulus ovalifolius sensu Grisebach, Fl. Brit. W. Indian Is. 474. 1862, non Vahl ex West, 1793.
Convolvulus obcordatus Millspaugh, Publ. Field Mus. Bot. **2**: 88. 1900.
Jacquemontia obcordata (Millspaugh) House, N. Y. State Mus. Bull. **233**: 63. 1921.
Jacquemontia subsalina Britton in Britton & Wilson, Sci. Survey Porto Rico Virgin Is. **6**: 106. 1925.

Prostrate plant, rooting occasionally at the nodes, more or less strigose with 2-armed hairs on stems, petioles, peduncles, and pedicels. Petioles about 1/2 length of blades; blades obcordate, fleshy, glabrous, 1–5 cm. long, margin slightly repand. Peduncles shorter or longer than subtending petioles, bearing (1 to) several flowers in umbels; bracts small; pedicel(s) filiform and nodding, ca. 5–8 mm. long; sepals unequal, about 3 mm. long, rounded on the outside sepal to acute on the inside; corolla rotate, ca. 7 mm. long, white, blue, or lavender, scarcely lobed; stigmas strap shaped. Capsule subglobose, straw colored, 2- or 4-valved; seeds 4, brown, very narrowly and unevenly winged on the margins.

GENERAL DISTRIBUTION. Mexico, Central America, West Indies.

DISTRIBUTION IN LESSER ANTILLES. St. Barts, Antigua, Guadeloupe, Marie Galante.

5. **Jacquemontia pentantha** (Jacq.) G. Don, Gen. Syst. **4**: 283. 1838 [1837?].

Convolvulus pentanthos Jacq. Collect. **4**: 210. 1791.
Convolvulus azureus Desr. in Lam. Encycl. Méth. Bot. **3**: 554. Feb. 1792; L. Richard, Actes Soc. Hist. Nat. Paris **1**: 107. 1792.
Convolvulus nummularius Vahl, Eclog. **2**: 13. 1798, non. L. 1753.
Convolvulus violaceus Vahl, Symb. Bot. **3**: 29. 1794.
Convolvulus canescens H.B.K. Nov. Gen. Sp. **3**: 99 (78 in folio ed.). 1818 [1819].
Jacquemontia violacea (Vahl) Choisy, Mém. Soc. Hist. Nat. Genève **8**: 61. 1837.
Jacquemontia azurea (Desr.) Choisy, *ibid.* 62.
Ipomoea canescens (H.B.K.) G. Don, Gen. Syst. **4**: 273. 1838 [1837?].
Jacquemontia canescens (H.B.K.) Bentham, Pl. Hartweg. 226. 1846.
Convolvulus umbellatus Sessé & Moçiño, Fl. Mex. ed. 2. 32. 1894.

Jacquemontia elongata Britton, Bull. Torrey Bot. Club **53:** 470. 1926.
Jacquemontia houseana Standley, Publ. Field Mus. Bot. **11:** 140. 1932.

COMMON NAMES. Liane bleue, calalou à dah (Guadeloupe); liseron bleu (Martinique).

Slender vine with many branches, glabrous or with pubescence usually sparse except on young parts, the trichomes 3-armed. Petioles slender, 1–4 cm. long in mature leaves; blades cordate or narrowly ovate, midrib up to 8 cm. long, surface sometimes gland-dotted, usually acuminate or acute at apex, occasionally truncate at base, margin entire (appearing glandular especially at tip). Peduncles much longer than subtending petioles, often longer than leaves; bracts membranous, lanceolate, varying in size, the lowest sometimes 1 cm. long or more; pedicels short; inflorescences cymose-corymbose; few to many flowers; calyx accrescent, the sepals unequal, ovate, acuminate, the 2 outermost largest, ca. 7 mm. long and 5 mm. wide, the exposed ones foliaceous; corolla usually clear blue with a white star, 1.5–2.5 cm. long, wide funnel shaped, flaring from the base, margin entire, petals only slightly mucronate; stamens and pistil exposed; stigmas rod shaped. Capsule ovoid, 4–5 mm. high, brown, completely enveloped by calyx, 8-valved, tardily dehiscent; seeds 4 or fewer, brown, wingless.

GENERAL DISTRIBUTION. Tropical America, Malaysia, Ceylon.

DISTRIBUTION IN LESSER ANTILLES. St. Martin, Barbuda, Saba, St. Eustatius, St. Kitts, Antigua, Montserrat, Guadeloupe, La Désirade, Marie Galante, Îles des Saintes, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Bequia, Mustique, Cannouan, Union, Grenada.

6. **Jacquemontia solanifolia** (L.) Hallier f. Bot. Jahrb. **16:** 542. 1893.

Ipomoea solanifolia L. Sp. Pl. **1:** 161. 1753.
Ipomoea filiformis Jacq. Enum. Pl. 13. 1760 (as *Ipomaea*).
Convolvulus filiformis (Jacq.) Desr. in Lam. Encycl. Méth. Bot. **3:** 555. 1792.
Convolvulus solanifolius (L.) Sprengel, Syst. Veg. **1:** 596. 1824.
Exogonium filiforme (Jacq.) Choisy, Mém. Soc. Hist. Nat. Genève **8:** 51. 1837.
Quamoclit solanifolia (L.) Choisy in DC. Prodr. **9:** 335. 1845.
Exogonium solanifolium (L.) Britton, Mem. Brooklyn Bot. Gard. **1:** 82. 1918.
Quamoclit filiformis (Jacq.) Roberty, Candollea **14:** 41. 1952.

COMMON NAME. Patate grand bois (Guadeloupe, Martinique).

Slender, twining stems, pubescent on very young parts with 3-armed hairs. Petioles up to 4 cm., usually ca. 1 cm. long; blades wide to narrowly ovate, midrib up to 6 cm., the apex usually obtuse or slightly retuse, mucronate, the base cordate, truncate, or rounded, the veins depressed above, the surface minutely gland-dotted, the margin entire. Peduncles longer than subtending petioles; inflorescences lax; flowers several; bracts minute; pedicel ca. 1 cm. long; sepals subequal, 3–4 mm. long, rounded to acute, usually slightly mucronate, glabrous except sometimes at the

apex, very narrowly scarious on the edges; corolla red-purple, 2–2.5 cm. long, the tube narrow, lobed, spreading only in the uppermost fifth; stamens and pistil exserted; stigmas subglobose. Capsule conical, ca. 5 mm. high, 8-valved; seeds 4 or fewer, dark brown, winged on 3 edges.

GENERAL DISTRIBUTION. Puerto Rico, Virgin Islands, Lesser Antilles.

DISTRIBUTION IN LESSER ANTILLES. Anguilla, St. Barts, St. Kitts, Antigua, Guadeloupe, Marie Galante, Désirade, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Prune Island.

7. **Jacquemontia tamnifolia** (L.) Grisebach, Fl. Brit. W. Indian Is. 474. 1862.

Ipomoea tamnifolia L. Sp. Pl. 162. 1753.
Convolvulus capitatus Desr. in Lam. Encycl. Méth. Bot. 3: 554. 1792.
Convolvulus ciliatus Vahl, Eclog. 2: 13. 1798.
Convolvulus tamnifolia (L.) G. F. W. Meyer, Primitiae Florae Essequeboensis, 95. 1818.
Convolvulus guineënsis Schumacher, Beskr. Guineiske Pl. 90. 1827.
Jacquemontia capitata (Desr.) G. Don, Gen. Syst. 4: 283. 1838 [1837?].
Ipomoea guineensis (Schumacher) G. Don, *ibid.* 269.
Thyella tamnifolia (L.) Raf. Fl. Tellur. 4: 84. 1838.
Ipomoea capitata (Desr.) Choisy in DC. Prodr. 9: 365. 1845.
Convolvulus praelongus S. Moore, Trans. Linn. Soc. London Bot. 4: 403. 1895.
Jacquemontia macrocephala Brandegee, Zoe 5: 219. 1905.
Thyella macrocephala (Brandegee) House, Muhlenbergia 5: 68. 1909.
Jacquemontia rondonii Hoehne, Anex. Mem. Inst. Butantan Bot. 1(6): 53. *t. 8.* 1922.
Jacquemontia mattogrossensis Hoehne, *ibid.* 54. *t. 9.*

COMMON NAME. Liseron savane (Guadeloupe).

Twining plant with hirsute to glabrate stems, sometimes flowering before twining begins. Hairs long, yellow, and 2-armed on stems, 2-armed or simple on leaves, simple and drying reddish brown on inflorescence. Petioles very short to as long as or longer than blades; blades cordate, sometimes cuneate within the basal sinus, sometimes gland-dotted on the upper surface, midrib up to 9 cm. long, apex usually acuminate, the margin entire, sometimes somewhat repand, sometimes ciliate. Peduncles sturdier and much longer than subtending petioles, often longer than the leaves; inflorescences very compressed, cymose corymbs, with numerous flowers surrounded by several foliaceous bracts; the 2 lowest bracts largest and opposite, lanceolate or ovate, up to 4 cm. long; sepals narrowly triangular, subequal, hirsute, ciliate, dentate from trichome bases, ca. 1 cm. long; corolla lavender-blue with a paler star, ca. 1.5 cm. long or less, funnel shaped, slightly lobed; stigmas strap shaped, slightly stalked. Capsule globose but somewhat flattened, ca. 4 mm. high, 8-valved; seeds 4, brown, wingless.

GENERAL DISTRIBUTION. Africa and the Mascarenes, tropical America.

DISTRIBUTION IN LESSER ANTILLES. Nevis, Guadeloupe, Dominica, Martinique, St. Vincent.

8. **Jacquemontia verticillata** (L.) Urban, Symb. Antill. 3: 339. 1902.

Ipomoea verticillata L. Syst. Nat. ed. 10. 924. 1759.
Convolvulus verticillatus (L.) L. Sp. Pl. ed. 2. 220. 1762.
Convolvulus parviflorus Desr. in Lam. Encycl. Méth. Bot. 3: 556. 1792.
Convolvulus polycarpus H.B.K. Nov. Gen. Sp. 3: 98 (77 in folio ed.). 1818 [1819].
Convolvulus micranthus R. & S. Syst. Veg. 4: 276. 1819.
Convolvulus plumerii Sprengel, Syst. Veg. 1: 602. 1824.
Ipomoea polycarpa (H.B.K.) G. Don, Gen. Syst. 4: 270. 1838 [1837?].
Jacquemontia micrantha (Desr.) G. Don, *ibid.* 283.
Convolvulus nodiflorus Desr. var. *deglabratus* Choisy in DC. Prodr. 9: 414. 1845.
Jacquemontia verticillata (L.) Urban var. *stenophylla* Urban, Symb. Antill. 3: 340. 1902.

Slender vine, pubescent, especially on young parts, with 3-armed trichomes; stems becoming glabrous with age. Petioles slender, ± 1 cm. long, blades narrowly ovate or oblong, midrib up to 4 cm. long, apex obtuse and mucronate, base cordate, margin entire or slightly repand. Peduncles very short; inflorescences compact cymes of many to few flowers; bracts very small; pedicels 3–4 mm. long; sepals subequal, acuminate, pubescent, 3–4 mm. long; corolla ca. 5 mm. long, pink or lavender, deeply lobed, lobes acute; stigmas broadly strap shaped. Capsule ca. 3 mm. high, globose, (4- or) 8-valved; seeds 4, brown, winged on 2 or 3 margins.

GENERAL DISTRIBUTION. Mexico, Central America, West Indies.

DISTRIBUTION IN LESSER ANTILLES. St. Vincent, Grenada, Cannouan.

5. **Aniseia** Choisy, Mém. Soc. Hist. Nat. Genève 6: 396. 1834.

Herbs twining or prostrate, scarcely branching, glabrous or glabrescent. Leaves short petiolate, linear to oblong-lanceolate, mucronate. Flowers axillary, solitary or few; bracts 2, very small; sepals unequal, enlarging in fruit, the outer 3 larger and often decurrent; corolla white, funnel shaped, with hairs on the outer surface of the convolvulaceous star; pollen smooth; stigma biglobose, ovary bilocular, ovules 4. Capsule 4-valved.

LECTOTYPE SPECIES: *Aniseia uniflora* (Burman f.) Choisy.

Aniseia martinicensis (Jacq.) Choisy, Mém. Soc. Hist. Nat. Genève 8: 66. 1837.

Convolvulus martinicensis Jacq. Select. Stirp. Am. Hist. 26. *t. 17.* 1763.
Convolvulus uniflorus Burman f. Fl. Indica, 47. *t. 21, fig. 2.* 1768.
Convolvulus salicifolius Desr. in Lam. Encycl. Méth. Bot. 3: 543. 1792.
?*Convolvulus emarginatus* Vahl, Symb. Bot. 3: 23. 1794.
Ipomoea martinicensis (Jacq.) G. F. W. Meyer, Primitiae Florae Esseqeboensis, 98. 1818.

Ipomoea uniflora (Burman f.) R. & S. Syst. Veg. **4:** 247. 1819.
Convolvulus rheedii Wall. in Roxb. Fl. Indica **2:** 70. 1824.
Convolvulus pterocarpus Bert. in Colla, Hortus Ripul. 37. 1824.
Aniseia uniflora (Burman f.) Choisy, Mém. Soc. Hist. Nat. Genève **6:** 483. *t. 2, fig. 9.* 1834.
Ipomoea pterocarpa (Bert.) Don, Gen. Syst. **4:** 282. 1838 [1837?].
Aniseia salicifolia (Desr.) Steudel, Nom. Bot. ed. 2. **1:** 99. 1841.
Jacquemontia chiapensis Brandegee, Univ. Calif. Publ. Bot. **6:** 60. 1914.

COMMON NAMES. Liseron savane, patate marron (Guadeloupe); petit liseron, patate marron (Martinique).

Annual 2–4 meters long with few branches, climbing or prostrate, growing in moist places, glabrous or with sparse, simple, golden hairs. Petioles short, up to 1 cm. long; blades elliptic, rounded at the apex, mucronate, ca. 6 cm. long. Flowers solitary or occasionally few; peduncle much longer than the subtending petiole, bearing 2 very small bracts at the base of each pedicel; sepals pubescent, acute to acuminate, the outer 3 decurrent, ovate, much larger than the inner 2; corolla white, funnel shaped, tapering to the base, twice as long as the calyx, the outer surface of the star covered with hairs, hairs at the rim forming tufts protruding from the points of the star; anthers bearing glandular vesicles, pollen smooth; stigma biglobose, ovary bilocular, ovules 4. Capsule brown, glabrous, 4-valved, the inner surfaces of the valves pearly smooth, cream colored; seeds very dark brown, with lighter, scaly hairs on the angles and around the hilum.

GENERAL DISTRIBUTION. The tropics.

DISTRIBUTION IN LESSER ANTILLES. Guadeloupe, Marie Galante, Martinique.

6. **Merremia** Dennstedt ex Endl. Gen. Pl. Suppl. 1: 1403. 1841, *nomen cons.*

Twiners, glabrous or pubescent, the hairs simple, sometimes glandular. Leaves palmately compound or simple, entire, pedate, or palmately lobed; petiole and peduncle usually long. Flowers axillary, solitary or few to several; bracts small; sepals subequal, usually glabrous, occasionally with hairs, usually stiff and shiny smooth, accrescent; corolla glabrous, white with or without a dark purple center, sometimes completely yellow, funnel shaped or campanulate, occasionally slightly lobed, the 5-pointed star usually well defined, often with marked longitudinal striations; stamens and pistil well included; anthers usually twisted after dehiscence, pollen smooth; stigma biglobose, ovary usually bilocular. Fruit a thin-walled capsule, usually surrounded by the enlarged and thickened calyx, dehiscing by 4 valves or irregularly; seeds (1 to) 4, angular or round depending on the number, pubescent or glabrous.

TYPE SPECIES: *Merremia hederacea* (Burman f.) Hallier f.

KEY TO THE SPECIES OF MERREMIA

1. Leaves simple; flowers yellow or white with dark center.
   2. Leaves cordate to hastate, entire to 3-lobed; calyx scarcely enlarged in fruit.
      3. Leaves more than 5 cm. long; flowers borne in umbels, 2–3 cm. long. ..... 6. *M. umbellata.*
      3. Leaves 1.5–5(–6) cm. long; flowers up to 1 cm. long, not borne in umbels. ..... 3. *M. hederacea.*
   2. Leaves very deeply 7-lobed; sepals much enlarged in fruit.
      4. Leaf lobes sinuate-dentate; flowers white with dark center; fruiting calyx ca. 5 cm. across. ..... 2. *M. dissecta.*
      4. Leaf lobes entire; flowers yellow; fruiting calyx ca. 10 cm. across. ..... 5. *M. tuberosa.*
1. Leaves compound, leaflets 5; flowers white.
   5. Stems and leaves hairy; leaflets entire; outer sepals hispid. ..... 1. *M. aegyptia.*
   5. Stems, leaves, and sepals glabrous; leaflets serrulate. ..... 4. *M. quinquefolia.*

1. **Merremia aegyptia** (L.) Urban, Symb. Antill. **4**: 505. 1910.

Ipomoea aegyptia L. Sp. Pl. **1**: 162. 1753.
Convolvulus pentaphyllus L. *ibid.* ed. 2. **1**: 223. 1762, excl. var. *serpens* L.
Ipomoea pentaphylla (L.) Jacq. Collect. **2**: 297. 1788.
Convolvulus nemorosus Willd. ex R. & S. Syst. Veg. **4**: 303. 1819.
Ipomoea pilosa Cav. Ic. Descr. Pl. **4**: 11. *t. 323.* 1797.
Batatas pentaphylla (L.) Choisy, Mém. Soc. Hist. Nat. Genève **6**: 436. 1834.
Spiranthera pentaphylla (L.) Bojer, Hortus Maurit. 226. 1837.
Merremia pentaphylla (L.) Hallier f. Bot. Jahrb. **16**: 552. 1893.
Ipomoea sinaloensis Brandegee, Zoe **5**: 217. 1905.
Operculina aegyptia (L.) House, Bull. Torrey Bot. Club **33**: 502. 1906.

COMMON NAMES. Noyeaux (St. Martin, Saba, St. Eustatius); liane poilue (Guadeloupe, Martinique).

Twiner with hispid stems sometimes becoming glabrous with age. Leaves palmately compound, petiole about equal to length of middle leaflet; leaflets 5, sessile, obovate to lanceolate, entire, middle one up to 14 cm. long and 6 cm. wide, lowest and smallest ones up to 9.5 cm. long and 4.5 cm. wide, midrib sunken above and raised below, the hairs yellow-brown, as long on petiole as on stem, shorter and fewer on blades, more numerous on lower surface, especially on the veins, apex acuminate, base cuneate. Peduncles longer than petioles, hairy; inflorescences lax dichasia of (1 to) 3 to 9 flowers; bracts 3–4 mm. long, narrowly triangular; pedicels 2–4 cm. long, hairy; buds sharply pointed; calyx upright, the sepals oblong, with obtuse apex, the outer 2 slightly larger, with the lower 2/3 conspicuously covered with long, stiff, patent, yellow-brown hairs, the exposed surfaces of inner ones also hairy at the base; corolla all white, campanulate, 3 cm. long, star well marked; stamens subequal, pollen smooth; ovary 4-locular, ovules 4. Capsule globose, not very thin walled, ca. 1 cm.

in diameter, dehiscing regularly by 4 valves, exposing septae extending to form a conical hood over the (1 to) 4 glabrous, brown seeds. Enlarged calyx spreading in fruit.

GENERAL DISTRIBUTION. Tropical America, Africa, Asia, Pacific Islands.

DISTRIBUTION IN LESSER ANTILLES. St. Martin, St. Barts, Saba, St. Eustatius, St. Kitts, Antigua, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Grenada.

2. **Merremia dissecta** (Jacq.) Hallier f. Bot. Jahrb. **16**: 552. 1893 (as *M. disecta*).

Convolvulus dissectus Jacq. Obs. Bot. **2**: 4. *t. 28*. 1767.
Ipomoea dissecta (Jacq.) Pers. in L. Syst. Veg. ed. 15. 207. 1797, in note, non Willd. 1794.
Ipomoea sinuata Ortega, Pl. Horti Regii Bot. Matrit. 84. 1798.
Ipomoea subpedata Desf. Cat. Pl. Horti Regii Paris. (Tableau de l'école Bot. ed. 3.) 397. 1829.
?*Ipomoea nigricans* Gardner, London Jour. Bot. **1**: 180. 1842.
Operculina dissecta (Jacq.) House, Bull. Torrey Bot. Club **33**: 500. 1906.

COMMON NAMES. Bini bini (Dutch islands); liane amande amère, liane à noyau, liane noyau, méné-vini (Guadeloupe); pâte d'amande, liane à noyau, méné-vini (Martinique).

Twiner; stems, petioles, and peduncles glabrous to hispid, the hairs simple, yellow. Leaves simple, petiole a little shorter than blade; blade very deeply pedately lobed, glabrous, often with numerous black dots on the lower surfaces, the lobes 7, sinuate-dentate, apex acute, extreme tip rounded and mucronate, the central lobe up to 7 cm. long and 4 cm. wide, slightly larger than side lobes (except the very lowest pair), lowest pair sometimes not developing. Peduncles 1–2 times length of petioles; flowers solitary, or few and the inflorescence lax, cymose; pedicel 1.5–3 cm.; bracts ca. 3 mm. long, triangular, caducous; buds nodding, triangular, sharply pointed; calyx upright in flower, the sepals cream colored, slightly fleshy, stiff, boat shaped, ovate, acute, spotted on the inside, thin on the edges, the outer 2 longer and thicker, 2–2.5 cm. long; corolla white with dark red to purple center, campanulate, ca. 4 cm. long, with well-marked striate star; anthers just within throat; ovary bilocular. Fruit nodding, surrounded by the brown, enlarged, spreading calyx, the sepals ca. 3 cm. long; capsule globose, ca. 1.5 cm. high, 4-valved, dehiscing regularly; seeds 4, glabrous, black.

GENERAL DISTRIBUTION. Tropical America; introduced into other tropical regions and sometimes becoming naturalized.

DISTRIBUTION IN LESSER ANTILLES. Anguilla, St. Martin, St. Barts, Saba, St. Eustatius, St. Kitts, Antigua, Montserrat, Guadeloupe, La Désirade, Marie Galante, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Bequia, Carriacou, Grenada.

3. **Merremia hederacea** (Burman f.) Hallier f. Bot. Jahrb. **18**: 118. 1894.

Evolvulus hederaceus Burman f. Fl. Indica, 77. *t. 30, fig. 2.* 1768.
Convolvulus flavus Willd. Sp. Pl. **1**: 852. 1797.
Merremia convolvulacea Dennst. Schlüssel Hortus Malab. 39. 1818, *nomen nudum.*
Convolvulus hederaceus sensu Merrill, Philip. Jour. Sci. Bot. **9**: 132. 1914, non L. 1753.

Slender twiner, rooting at and between nodes in contact with soil; stem glabrous or pubescent especially at nodes, occasionally tuberculate. Petioles usually tuberculate, pubescent on grooved upper side; blades simple, cordate, entire to three lobed and coarsely toothed on lower lobes, the midrib 1.5–4(–5) cm. long, equal to or longer than petiole, the lower surface glabrous, the upper surface sparsely strigose, especially on nerves, or sometimes glabrous, the apex acute to acuminate, mucronate. Peduncles shorter than petioles to exceeding length of leaves; inflorescences 3- to many-flowered cymes, occasionally flowers solitary; bracts small, scalelike, caducous; calyx usually smooth and shiny, the sepals subequal, mucronate, the outer ones truncate, the inner ones tridentate, larger, ca. 5 mm. long; corolla yellow, ca. 8 mm. long, campanulate, star well defined by striations; stamens reaching to margin of corolla; stigma biglobose, exserted, ovary 2-celled, style persistent. Fruit ca. 5 mm. tall, depressed-globose and transversely wrinkled below, conical above with lighter-colored, dimpled apex, splitting first into 2 valves and later into 4; seeds 4, dark brown, with 1 curved and 2 flat surfaces, pubescent, hairs longer on the edges; calyx deflexed in mature fruit.

General distribution. Old World tropics; introduced into Cuba and the Lesser Antilles.

Distribution in Lesser Antilles. Guadeloupe, Grande Terre, Grands Fonds, mare de Champvert, *Fournet H-1850, H-2137* (P). This is being treated as a new record for the Lesser Antilles, although it may have been growing in the St. Vincent Botanic Garden almost 200 years ago under the name *Convolvulus flavus.* We have no way of knowing whether the garden plant was *Convolvulus flavus* Willd. (1797) or *C. flavus* Salisbury (1796), the latter being a synonym of *Merremia umbellata.*

4. **Merremia quinquefolia** (L.) Hallier f. Bot. Jahrb. **16**: 552. 1893.

Ipomoea quinquefolia L. Sp. Pl. **1**: 162. 1753.
Convolvulus quinquefolius (L.) L. Syst. Nat. ed. 10. 923. 1759.
Batatas quinquefolia (L.) Choisy, Mém. Soc. Hist. Nat. Genève **8**: 49. 1837.

Common name. Patate marron (Guadeloupe).

Stems twining, glabrous or with long, patent hairs. Leaves palmately compound, petiolate, petiole up to 5 cm. long; leaflets 5, sessile, glabrous,

lanceolate, serrulate, the midribs raised on lower surfaces, each extended into a mucro, the middle leaflet longest, up to 7 cm. long and 2 cm. wide. Peduncles equal to or longer than subtending leaves; upper portion of peduncle and occasionally pedicel with numerous glandular hairs; bracts ca. 1.5 mm. long, triangular, often mucronate; buds pointed; flowers opening before subtending leaf matures, usually in cymose groups of 3 or 5, occasionally solitary; sepals light green, darker in the center and toward mucro, unequal, stiff, glabrous, the outer 2 shorter, oblong-ovate to triangular, ca. 5.5 mm. long, 3 mm. wide at base, narrower above, emarginate, with a mucro at apex, the inner 3, 7.5–8 mm. long, 3 mm. wide, oblong, boat shaped, auriculate at base, rounded at apex with a small mucro in the middle, the calyx accrescent in fruit; corolla white or cream, funnel shaped, 2 cm. long or more; ovary 4-celled with 4 ovules, style slender, persistent. Capsule depressed-globose, beaked or with entire style attached, straw colored with yellow veining on outer surface, dehiscing into 4 valves; septae 4, transparent, persistent; seeds 4, brown, smooth, covered with scalelike hairs.

GENERAL DISTRIBUTION. Tropical America.

DISTRIBUTION IN LESSER ANTILLES. St. Barts, Antigua, Guadeloupe, Martinique, Barbados, Grenada.

Compare the solitary flowers on spiraled peduncles and the entire leaflets of *Ipomoea wrightii*.

5. **Merremia tuberosa** (L.) Rendle in Dyer, Fl. Trop. Afr. 4(2): 104. 1905.

Ipomoea tuberosa L. Sp. Pl. **1**: 160. 1753.
Ipomoea mendesii Welw. Apont. Phytogeogr. in Ann. Conselho Ultramar. **55**: 584. 1859.
Operculina tuberosa (L.) Meissner in Martius, Fl. Brasil. **7**: 212. 1869.

COMMON NAMES. Liane jaune, liane à tonnelle, liane à courtine, bois patate, rose de Jéricho (Guadeloupe).

Stout climber, glabrous throughout; roots tuberous. Petioles as long as blades or longer; leaves simple; blade up to 14 cm. long, deeply palmately lobed, the lobes 7, occasionally 5, entire, lanceolate, acuminate at apex, largest lobe in the middle, grading down to the smallest at the bottom on either side, the midrib and primary veins raised on the lower surface, midribs of uppermost pair of lobes usually branching pinnately from the central midrib, those of the lower ones branching palmately. Peduncles about as long as the petioles, accrescent; flowers solitary, or several in a lax dichasium; bracts triangular, ca. 2 mm. long, falling very soon; pedicel tapering, ca. 1 cm. long in flower, attaining 3–4 cm. in fruit; pedicel and peduncle becoming woody; sepals ovate, rounded at the apex, 2–3 cm. long, the outer 2 thicker and wider than the others; corolla yellow, ca. 5 cm. long, funnel shaped, reflexed at the margin; pistil tapering, persistent,

ovules large. Capsule straw colored, ca. 3 cm. tall, globose, thin walled, appearing 4-valved but usually dehiscing irregularly and coming loose at the base; fruit surrounded by spreading, accrescent sepals, up to 6 cm. long, woody, striate, brown on the outside, cream colored and shiny on the inside; seeds (1 to) 4, black, hairy, shape depending on number.

GENERAL DISTRIBUTION. Tropical America, Africa, Mascarene Islands, India, Ceylon; cultivated in Hawaii and Malaysia. Probably native to tropical America.

DISTRIBUTION IN LESSER ANTILLES. Guadeloupe, Martinique, St. Lucia (cultivated).

6. **Merremia umbellata** (L.) Hallier f. subsp. **umbellata** Ooststr. & Hoogland, Fl. Males. I. 4(4): 449. 1953.

Merremia umbellata (L.) Hallier f. Bot. Jahrb. **16:** 552. 1893.
Convolvulus umbellatus L. Sp. Pl. **1:** 155. 1753.
Convolvulus multiflorus Miller, Gard. Dict. ed. 8. [alph. ord.] 1768.
Convolvulus aristolochiaefolius Miller, *ibid.*
Convolvulus flavus Salisbury, Prodr. 124. 1796.
Ipomoea umbellata (L.) G. F. W. Meyer, Primitiae Florae Essequeboensis, 99. 1818.
Convolvulus caracasanus R. & S. Syst. Veg. **4:** 301. 1819.
Ipomoea polyanthes R. & S. *ibid.* 234.
Convolvulus sagittifer H.B.K. Nov. Gen. Sp. **3:** 100 (79 in folio ed.). 1818 [1819].
Ipomoea sagittifera (H.B.K.) G. Don, Gen. Syst. **4:** 273. 1838 [1837?] (as *sagittifer*).
Ipomoea primulaeflora G. Don, *ibid.* 270.
Convolvulus densiflorus Hooker, Bot. Beechey's Voy. 303. 1838.
?*Ipomoea cymosa* (Desr.) R. & S. var. *culta* Choisy in DC. Prodr. **9:** 371. 1845.
Convolvulus luteus Martens & Gal. Bull. Acad. Bruxelles **12:** 260. Sept. 6, 1845.
Ipomoea micans Garcke, Linnaea **22:** 66. 1849.
Ipomoea mollicoma Miq. Stirpes Surinam. Selec. 132. *t. 37.* 1850.
Merremia umbellata (L.) Hallier f. var. *occidentalis* Hallier f. Versl. Buitenzorg s'Lands Plant. **1895:** 127. 1896.
Merremia umbellata (L.) Hallier f. var. *umbellata* Hallier f. Bull. Soc. Bot. Belg. **35:** 270. 1896.
Merremia rondoniana Hoehne, Anex. Mem. Inst. Butantan Bot. **1**(6): 60. *t. 13.* 1922.

COMMON NAMES. Liane à berceau, liane-berceau, liane à malingres (Guadeloupe); liane douce jaune, fleur patate jaune, liane à tonnelle (Martinique); hog vine (Barbados).

Twiner, occasionally prostrate and rooting at the nodes, glabrous to pubescent, the hairs simple, white to pale yellow. Leaves simple, stipulate, the stipule small, size variable; petiole ½–1½ times length of midrib; blade cordate, sagittate, or occasionally hastate, entire, to 17 cm. long and

12 cm. wide, palminerved, midrib sunken above, all veins prominent beneath, when pubescent, hairs more numerous along nerves, the apex obtuse to acuminate, sometimes emarginate, mucronate. Peduncles usually thicker and much longer than subtending petioles, sometimes winged; flowers numerous to few, in umbels or congested cymes; bracts small, of varying lengths, linear, caducous; pedicels 1–2 cm. long; buds blunt; sepals subequal, a little less than 1 cm. long, stiff, thin on the edges, widely elliptic, boat shaped, rounded at the apex, mucronate; corolla yellow, funnel shaped, 2–3 cm. long, star well marked but not striate; ovary bilocular, ovules 4, style persistent. Capsule globose, 4-valved, brown, dehiscing regularly; sepals separating somewhat, not very much larger than in flower, forming a cup around the base of the capsule; seeds 4, dark brown, pubescent, especially on angles.

GENERAL DISTRIBUTION. Tropical America, West Africa, occasionally in the Far East where it has been introduced.

DISTRIBUTION IN LESSER ANTILLES. St. Barts, Antigua, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Bequia, Grenada.

The Old World *Merremia umbellata* subsp. *orientalis* (Hallier f.) Ooststr. has long hairs on the seeds and usually has white flowers.

7. **Operculina** Silva Manso, Enum. Subst. Brazil. 16. 1837.

Twining plants with perennial stems; stems, petioles, peduncles, and pedicels often winged. Leaves entire or lobed. Peduncles longer than subtending petioles; pedicels wider at the top; calyx large, often not green, pear shaped in bud; calyx and pedicel enlarged in fruit; corolla campanulate or wide funnel shaped, white, yellow, or purple; pollen smooth; stigma biglobose, ovary bilocular, ovules 4. Capsule with exocarp separating as operculum, dehiscence or remainder of wall regular or irregular; seeds 4, pubescent or smooth.

TYPE SPECIES: *Operculina turpethum* (L.) Silva Manso.

KEY TO THE SPECIES OF OPERCULINA

1. Leaves palmately lobed. ..... *3. O. macrocarpa.*
1. Leaves not palmately lobed.
   2. Stems without wings; flowers white. ..... *4. O. ventricosa.*
   2. Stems winged; flowers not white.
      3. Leaves and stems pubescent; corolla violet; inflorescence 5- to 8-flowered. ..... *2. O. leptoptera.*
      3. Leaves and stems glabrous or glabrescent; corolla yellow; flower usually solitary. ..... *1. O. alata.*

1. **Operculina alata** (Ham.) Urban, Symb. Antill. 3: 343. 1902.

Convolvulus alatus Ham. Prodr. 24. 1825.
Ipomoea hamiltoni G. Don, Gen. Syst. 4: 268. 1838 [1837?].

Ipomoea alulata Miquel, Linnaea **18:** 599. 1844.
Ipomoea altissima Martius ex Choisy in DC. Prodr. **9:** 359. 1845.
Ipomoea pterodes Choisy in DC. *ibid.* 361.
Operculina pterodes (Choisy) Meissner in Martius, Fl. Brasil. **7:** 213. 1869.
Operculina altissima (Choisy) Meissner in Martius, *ibid. pl. 75.*

Climber with stems usually winged. Petioles 1–3 cm. long; blades acuminate, 5 cm. wide, glabrous or glabrescent, midrib up to 9 cm. long, apex mucronate, base cordate, the margin entire, sometimes 3-lobed. Peduncles winged, much longer than subtending petioles, usually bearing a single flower; bracts lanceolate, acuminate, ca. 1 cm. long; pedicels becoming thickened and 5-angled in fruit; buds pear shaped, acute; calyx large, bracts and sepals scarious, in dry material reddish brown, the sepals 2.5–3 cm. long, obtuse, mucronate, becoming more coriaceous in fruit; corolla yellow, campanulate, twice the length of the calyx. Capsule globose, ca. 1 cm. high, splitting irregularly, enveloped by the calyx; seeds 4, black, smooth.

GENERAL DISTRIBUTION. Tropical America.

DISTRIBUTION IN LESSER ANTILLES. Dominica, St. Vincent, Grenada.

2. **Operculina leptoptera** Urban, Symb. Antill. **3:** 342. 1902.

Climber with winged stems, wings arising from decurrent petioles; stems bearing short, appressed hairs. Petioles (0.8–)3 cm. long, long patent-pilose; blades triangular-ovate, 8 cm. long, 5–6 cm. wide, minutely pubescent on both surfaces, especially on the nerves beneath, the apex acute or somewhat obtuse, mucronate, the base deeply cordate, the margin entire. Peduncles 3.5–5 cm. long, scarcely winged; inflorescences corymbose, 5- to 8-flowered; bracts lanceolate-oblong or oblong, shortly acuminate, (10–)17 mm. long; pedicels 3–3.5 cm. long; sepals yellow-green, 17–22 mm. long, the outer ones longer, smoothly tomentose; corolla violet, 5–5.5 cm. long.

GENERAL DISTRIBUTION. Endemic to Martinique, this was originally described from a single specimen. To our knowledge, it has not been collected again. It is the only *Operculina* in the Lesser Antilles that is entirely pubescent and the only one with violet flowers. *Operculina triquetra* (Vahl) Hallier f. of St. Thomas and St. Croix is pubescent and has white flowers.

3. **Operculina macrocarpa** (L.) Urban, Symb. Antill. **3:** 343. 1902.

Convolvulus macrocarpus L. Syst. Nat. ed. 10. 923. 1759.
Convolvulus operculatus Gomez, Mem. Math. Phis. Acad. Real Sci. Lisboa **3:** Obs. 1. *t. 27, fig. 3.* 1812.
Ipomoea operculata (Gomez) Martius in von Spix & Martius, Reise Brasil. **2:** 547. 1828.
Operculina convolvulus Silva Manso, Enum. Subst. Brazil. 12. 1837.

Woody climber; stems winged, 4-sided. Petioles 2.5–7.5 cm. long, decurrent on stem; blades 3- to 7-lobed, divided all the way to the base or not completely, lobes 3.5–10 cm. long, attenuate at both ends, entire. Peduncles winged, longer and stouter than subtending petioles, with 1 or 2 flowers; bracts caducous; pedicels 2–4 cm. long, winged; sepals elliptic, obtuse, 1.5–2.5 cm. long, straw colored; corolla white, 4–5 cm. long, campanulate. Capsule depressed-globose, 2.5–4 cm. in diameter, surrounded by calyx, furrowed above, dehiscence irregular; seeds black, smooth.

GENERAL DISTRIBUTION. Brazil, Cuba, Lesser Antilles.

DISTRIBUTION IN LESSER ANTILLES. Guadeloupe, Martinique.

4. **Operculina ventricosa** (Bert.) Peter in Engler & Prantl, Nat. Pflanzenfam. 4(3a): 32. 1891.

Convolvulus ventricosus Bert. in Colla, Hortus Ripul. 37. 1824.
Ipomoea ventricosa (Bert.) G. Don, Gen. Syst. 4: 274. 1838 [1837?].
Operculina grandiflora sensu House, Muhlenbergia 5: 69. 1909, p. p., non *Convolvulus grandiflorus* Jacq. 1777.

COMMON NAMES. Hoofdpijnblad (St. Eustatius, Saba, St. Martin); liane blanche, liane d'argent (Guadeloupe); liane serpent, liane bord de mer (Martinique).

Climber with many long branches, glabrous or pubescent on young parts. Petioles slender, ca. 5 cm. long; blades large, broadly cordate, up to 16 cm. long, glabrescent, hairs chiefly on nerves below, apex acuminate and mucronate. Peduncles longer than subtending petioles, stout, pubescent, bearing 1 or more flowers in cymes; bracts oblong, acuminate, 2–3 cm. long; pedicels thickened above, angular, pubescent, becoming much enlarged in fruit; calyx glabrescent, the sepals ovate, obtuse, mucronate, 2.5–3.5 cm. long, membranous, accrescent; corolla expanding directly beyond the calyx into a broadly funnel-shaped limb, white or cream, 5–7.5 cm. long. Capsule globose, membranous, ca. 2.5 cm. in diameter, enclosed by calyx, splitting irregularly (herbarium material); seeds 4, black, glabrous, smooth.

GENERAL DISTRIBUTION. Lesser Antilles, Virgin Islands, Marianas Islands (Micronesia); cultivated in Hispaniola (perhaps escaped), Puerto Rico, Surinam.

DISTRIBUTION IN LESSER ANTILLES. St. Martin (*fide* Broeders), St. Barts, Saba, St. Eustatius (cultivated), Antigua, Guadeloupe, Martinique.

First described as cultivated in Guadeloupe (brought from St. Barts), this species is often cultivated in the French and Dutch islands. There are different opinions concerning the mode of dehiscence of its fruit: some authors think that it is by valves; others, that it is irregular. In material seen (St. Croix, *Fosberg 55369*), the fruit had split irregularly, although valves were clearly marked and the operculum had detached.

The Micronesian material is distinguishable by its smaller flowers and

by its larger and much more conspicuous, orbicular to ovate, somewhat persistent bracts. It is a more vigorous form, much more recently reported, and spreads rapidly (Fosberg & Sachet, 1977, p. 29).

8. **Ipomoea** L. Sp. Pl. 1: 159. 1753; Gen. Pl. ed. 5. 76. 1754.

Prostrate or twining plants, occasionally erect shrubs, glabrous or with hairs. Leaves simple, lobed, or palmately compound. Flowers axillary, 1 to many; bracts various, usually small and caducous; calyx very variable, persistent; corolla showy, red, blue, purple, pink, cream, or white, often with a dark center, funnel shaped, campanulate, or salver shaped, star well marked; stamens and pistil exserted or included; pollen round and spiny; ovary 2- to 4-celled, style 1, stigma capitate, simple or lobed. Fruit a valvate capsule; seeds 4 to 6 or fewer, brown or black, hairy or smooth.

TYPE SPECIES: *Ipomoea pes-tigridis* L. (prop. cons.).

KEY TO THE SPECIES OF IPOMOEA

1. Upright shrub with showy, pink-lilac flowers; cultivated. . . . . *I. carnea* Jacq. subsp. *fistulosa* (Martius ex Choisy) Austin.
1. Creeping or twining plant.
   2. Leaves pinnately many lobed, appearing compound; sometimes cultivated. . . . . 14. *I. quamoclit.*
   2. Leaves not pinnately many lobed.
      3. Leaves less than 2 cm. long, produced with flowers on short shoots. . . . . 5. *I. eggersiana.*
      3. Leaves more than 2 cm. long; no short shoots produced with flowers.
         4. Leaves palmately lobed or palmately compound.
            5. Leaves of axillary buds developed to look like stipules. . . . . 4. *I. cairica.*
            5. Leaves of axillary buds not developed.
               6. Leaves palmately compound.
                  7. Leaflets often lobed; peduncle threadlike, usually spiraling; corolla lilac, ca. 2 cm. long. . . . . 24. *I. wrightii.*
                  7. Leaflets not lobed; peduncles thick and straight; flowers large, dark red; cultivated. . . . . *I. horsfalliae* Hooker.
               6. Leaves palmately lobed.
                  8. Climbing plant; buds and sepals rounded. . . . . 9. *I. mauritiana.*
                  8. Creeping plant; buds pointed; sepals acuminate; cultivated. . . . . *I. batatas* (L.) Lam.
         4. Leaves simple or lobed, but not palmately so.
            9. Leaf apices blunt, rounded, retuse, or bilobed.
               10. Leaves oblanceolate or obtriangular. . . 17. *I. sphenophylla.*
               10. Leaves otherwise.
                  11. Leaves no more than 1.5 times as long as broad.
                     12. Leaves emarginate to bilobed, base cuneate or truncate; fruits about 1.5 cm. long. . . . . 12. *I. pes-caprae* subsp. *brasiliensis.*

12. Leaves reniform to cordate; fruit less than 1 cm. long. . . . . 3. *I. asarifolia.*
11. Leaves much longer than wide, base truncate to cuneate. . . . . 18. *I. stolonifera.*

9. Leaf apices acute to acuminate.
13. Plants prostrate, frequently rooting from the stem.
14. Leaves 1–5 times as long as wide; sepals rounded to acute; aquatic. . . . . 2. *I. aquatica.*
14. Leaves usually wider than long; sepals acuminate; producing ground tubers; cultivated. . . . . I. *batatas* (L.) Lam.

13. Plants climbing or creeping, not usually rooting along the stem.
15. Plants with conspicuous bracts and winged sepals. . . . . 16. *I. setifera.*
15. Plants otherwise.
16. Sepals ending in prolonged tips equal to half the length or more.
17. Sepals 6 mm. long; flowers red; stems not muricate. . . . . 6. *I. hederifolia.*
17. Sepals more than 6 mm. long; flowers not red; stems often muricate.
18. Prolonged tips on 3 outer sepals only; flowers white, tube 8 cm. long or more. . . . . 1. *I. alba.*
18. Prolonged tips not restricted to 3 outer sepals; flowers lilac, tube less than 8 cm. long. . . . . 22. *I. turbinata.*

16. Sepals sometimes mucronate but not extending into prolonged tips.
19. Sepals rounded or obtuse at the apex.
20. Sepals shortly mucronate; flowers usually solitary, white, with a long, narrow tube. . . . . 8. *I. macrantha.*
20. Sepals not mucronate; flowers usually in large, lax inflorescences, not white, tube not very narrow.
21. Sepals only subequal; corolla limb completely lobed. . . 15. *I. repanda.*
21. Sepals distinctly unequal; corolla limb not lobed.
22. Outer sepals larger than inner ones. . . . . 13. *I. phyllomega.*
22. Outer sepals smaller than inner ones. . . . . 23. *I. walpersiana.*

19. Sepals acute or acuminate.
23. Sepals less than 1 cm. long.
24. Sepals bordered with white edge; flowers 5 cm. or more long, blue. . . . . 20. *I. tricolor.*

24. Sepals not bordered with white edge; flowers less than 5 cm. long, not blue.
    25. Sepals ciliate and/or hirsute below; flowers pink-purple. . . . . 21. *I. triloba.*
    25. Sepals glabrous or pubescent; flowers white or cream with dark center. . . 11. *I. obscura.*
23. Sepals ca. 1 cm. long or more.
    26. Sepals ca. 1 cm. long; flowers pale lilac. . . . . 19. *I. tiliacea.*
    26. Sepals 2 cm. or more; flowers blue.
        27. Sepals broad and covered with hairs below, the upper portion long, narrow, and upright. . . . . 10. *I. nil.*
        27. Sepals unequal, usually curling, the outer ovate, the innermost almost linear. . . . . 7. *I. indica* var. *acuminata.*

1. **Ipomoea alba** L. Sp. Pl. 1: 161. 1753.

Convolvulus aculeatus L. *ibid.* 155, non *Ipomoea aculeata* Blume, 1825.
Ipomoea bona nox L. *ibid.* ed. 2. **1:** 228. 1762, *nomen illegit.*
Convolvulus grandiflorus L. f. Suppl. Pl. 136. 1781, non Jacq. 1777.
Convolvulus latiflorus Desr. in Lam. Encycl. Méth. Bot. **3:** 561. 1792.
Convolvulus bona-nox (L.) Sprengel, Syst. Veg. **1:** 600. 1824.
Convolvulus pulcherrimus Vell. Fl. Flum. **1:** 72. 1825; *ibid.*, Icones **2:** *t. 54.* 1827.
Calonyction speciosum Choisy, Mém. Soc. Hist. Nat. Genève **6:** 441. *t. 1, fig. 4.* 1834.
Convolvulus muricatus Blanco, Fl. Filip. 92. 1837.
Convolvulus bona-nox (L.) Bojer, Hortus Maurit. 227. 1837.
Calonyction megalocarpum A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba **11:** 129. 1850.
Calonyction pulcherrimum Parodi, Contr. Fl. Paraguay, 12. 1877.
Ipomoea aculeata (L.) Kuntze, Rev. Gen. Pl. **2:** 442. 1891.
Calonyction aculeatum (L.) House, Bull. Torrey Bot. Club **31:** 509. 1904.

COMMON NAMES. Belle de nuit, liane blanche bord de mer (Guadeloupe); fleur de nuit, liane douce (Martinique).

Glabrous creeper; stems often bearing small, recurved prickles. Petioles long, up to 20 cm.; blades large, membranous, midrib up to 16 cm., base deeply cordate, apex acuminate, margin entire. Peduncles as long as petioles or shorter; flowers solitary or few; pedicel(s) 1–2 cm. long; sepals keeled, the outer 3 smaller but each with a very long tip, the inner 2 rounded and mucronate; corolla tube green, up to 10 cm. long and very narrow, the limb white, about as wide as length of tube; stamens and pistil exserted. Pedicel thickening and becoming distinctly angular in

fruit; sepals turning back as the 4 horny valves of capsule dehisce; capsule conical and beaked, 2-celled; seeds 4, dark brown, smooth.

GENERAL DISTRIBUTION. This tropical American plant, usually growing in coastal areas, has become naturalized throughout the tropics.

DISTRIBUTION IN LESSER ANTILLES. St. Barts (cultivated), Guadeloupe, Dominica, Martinique, St. Vincent, Bequia.

2. **Ipomoea aquatica** Forskål, Fl. Aegypt.-Arab. 44. 1775.

Convolvulus repens Vahl, Symb. Bot. **1**: 17. 1790, non L. 1753.
Ipomoea reptans Poiret in Lam. Encycl. Méth. Bot. Suppl. **3**: 460. 1814, non *Convolvulus reptans* L. 1753.
Ipomoea repens Roth, Nov. Pl. Sp. 110. 1821, *quoad descr.*, non *Convolvulus repens* L. 1753, nec *Ipomoea repens* Lam. 1791.
Ipomoea subdentata Miq. Fl. Indiae Batavae **2**: 614. 1857.

Herb trailing in mud or floating in fresh or brackish water; stems glabrous, striate, thick, hollow or spongy, sometimes rooting at the nodes. Petioles mostly longer than blades; blades thin, sagittate, hastate, or cordate, up to 15 cm. long, typically much narrower than long, the apex usually acuminate, mucronate. Peduncles bearing 1 to few flowers; pedicels sometimes considerably longer than peduncles; bracts very small; sepals more or less equal, 7–8 mm. long, ovate, obtuse to acute; corolla funnel shaped, pale pink or lilac, with a darker center (white flowered in some Asian material), ca. 5 cm. long. Capsule globose, ca. 1 cm. wide, slightly pointed at the apex, 2-celled; seeds 4 or fewer, silky (those examined immature, without hairs).

GENERAL DISTRIBUTION. Native of Far East tropics; sometimes cultivated as a vegetable; distributed throughout the tropics. (Used as a vegetable in Trinidad.)

DISTRIBUTION IN LESSER ANTILLES. Guadeloupe, Mare Caybo, 2.5 km. SW. of Le Moule, *Proctor 19949* (A); St. François mare, *Rodriguez 4224* (P); mares acalines, Anse Bertrand, *Stehlé 1584* (GH).
Not previously reported from the Lesser Antilles.

3. **Ipomoea asarifolia** (Desr.) R. & S. Syst. Veg. **4**: 251. 1819.

Convolvulus asarifolius Desr. in Lam. Encycl. Méth. Bot. **3**: 562. 1792.
Ipomoea repens Lam. Tabl. Encyl. Méth. **1**: 467. 1791 [1793].
Convolvulus rugosus Rottler, Ges. Naturf. Freunde Berlin Neue Schr. **4**: 196. 1803.
Ipomoea beladamboe R. & S. Syst. Veg. **4**: 233. 1819.
Convolvulus beladambu (R. & S.) Sprengel, Syst. Veg. **1**: 608. 1824.
Convolvulus flagelliformis Roxb. Fl. Indica **2**: 68. 1824.
Ipomoea rugosa (Rottler) Choisy, Mém. Soc. Hist. Nat. Genève **6**: 446. 1834.
Ipomoea urbica Choisy in DC. Prodr. **9**: 349. 1845.
Convolvulus urbicus Salzm. ex Choisy in DC. *ibid.* 350, in synon.

Fleshy, creeping herb (dried stems hollow) of seashore and low ground near shore, sometimes with upright branches. Petioles grooved on the upper side, about as long as blades, with 2 glands at the upper end; blades reniform to cordate, 4–7(–10) cm. long and as wide. Peduncles usually as long as petioles; flowers (1 to) several; sepals in open flowers unequal, mucronate, oblong, blunt at the apex, the outer 2 thicker and about half as long as the membranous inner 3 (up to 14 mm.); corolla funnel shaped, rose-purple, 4–7 cm. long. Capsule globose, 1 cm. across, beaked, 2-celled; seeds 4, brown, smooth (immature material seen).

GENERAL DISTRIBUTION. Tropical America, Africa, Asia, Malaysia.

DISTRIBUTION IN LESSER ANTILLES. "Danish and French islands" (*fide* Grisebach), Martinique, St. Lucia.

4. **Ipomoea cairica** (L.) Sweet, Hortus Brit. 287. 1827.

Convolvulus cairicus L. Syst. Nat. ed. 10. 922. 1759.
Ipomoea palmata Forskål, Fl. Aegypt.-Arab. 43. 1775.
Convolvulus tuberculatus Desr. in Lam. Encycl. Méth. Bot. **3:** 545. 1792.
Ipomoea stipulacea Jacq. Pl. Rar. Horti Caes. Schoenbr. **2:** 39. *t. 199.* 1797.
Ipomoea pendula R. Br. Prodr. 486. 1810.
Ipomoea tuberculata (Desr.) R. & S. Syst. Veg. **4:** 208. 1819.
Ipomoea cavanillesii R. & S. *ibid.* 214.
Ipomoea bouvetti Duch. & Walp. Linnaea **23:** 752. 1850.
Convolvulus paniculatus Naves in Blanco, Fl. Filip. ed. 3. **1:** 131 and illustr. opp. 1877, non L. 1753.

COMMON NAME. Liane à tonnelle (Guadeloupe).

Perennial climber or creeper; stems becoming straw colored and warty, later wrinkled. Petioles slender, 1–6 cm. long; blades palmately compound or nearly so, leaflets 5, the lowest two sometimes 2-lobed, the middle one sometimes 3-lobed; leaflets and lobes ovate or ovate-lanceolate, the apex acute to rounded, mucronate, the base attenuate; small leaves on axillary shoots appearing as stipules. Peduncles usually short, 1- to several-flowered; bracts minute; sepals subequal or the outer ones shorter, rounded at the apex, scarious on the edges, 5–8 mm. long; corolla funnel shaped, lilac with tube purple inside, up to 7 cm. long. Capsule brown, smooth, ca. 1 cm. in diameter, 4-valved, 2-celled; seeds 4 or fewer, very dark brown, woolly, with long, light, silky hairs on edges.

GENERAL DISTRIBUTION. This African species has been widely cultivated in the tropics and has escaped.

DISTRIBUTION IN LESSER ANTILLES. Guadeloupe, Barbados, Grenada.

West Indian material never seems to have the tomentose leaf axils of African material. In addition, West Indian specimens have fewer flowers per inflorescence and rarely, if ever, set fruit.

5. **Ipomoea eggersiana** Peter in Engler & Prantl, Nat. Pflanzenfam. 4(3a): 30. 1891.

Ipomoea arenaria sensu Urban, Symb. Antill. **4:** 508. 1910, p. p., non R. & S. 1819.

Exogonium eggersii House, Bull. Torrey Bot. Club **35:** 104. *pl. 2a.* 1908.

Slender, glabrous, trailing or twining vine. Leaves small, 1 cm. long or less, very variable, from simple and ovate to 6-lobed, more often with the apex emarginate and mucronate, the base truncate and with 2 pronounced basal lobes; 2 to several leaves borne on a short shoot at each node. Peduncles usually less than 1 cm. long; flowers solitary; calyx 5–6 mm. long, the sepals rounded, subequal; corolla campanulate to broadly funnel shaped, ca. 4 cm. long, green on the outside of the tube, pink, lilac or almost white on the limb, conspicuous among the very small leaves. Capsule ovoid, brown, 1 cm. high, 4-valved, inside of valve straw colored and shiny, septum opaque; seeds 4, dark brown, with long, silky, brown hairs on the end opposite the hilum.

GENERAL DISTRIBUTION. Virgin Islands, Lesser Antilles.

DISTRIBUTION IN LESSER ANTILLES. Anguilla, St. Martin.

A plant of dry coastal thickets, *Ipomoea eggersiana* is remarkably like *I. steudelii* Millsp. of Puerto Rico; both are usually determined as *Ipomoea arenaria* (Choisy) Steudel or *Exogonium arenarium* Choisy. The leaves are alike and are borne on similar short shoots; the fruits and seeds are indistinguishable. The flowers differ, however: the Puerto Rican plant has scarlet, more salver-form flowers; the limb is recurved, with stamens and pistil exserted; the peduncles and calyx are longer, and the inner sepals are more obviously longer than the outer ones.

Choisy (Convolv. Rar. 51. *fig. 1.* 1837) gave the distribution of his species as Puerto Rico, St. Thomas, St. Domingue, and the Bahamas. The illustration accompanying his description, however, was of the Puerto Rican plant; it was clearly the Bertero specimen (lectotype, G-DC) from Puerto Rico that Choisy cited later in De Candolle's *Prodromus* (9: 347. 1845). Millspaugh (Field Mus. Publ. Bot. Ser. 2: 86. 1900) renamed the taxon *Ipomoea steudeli*, *I. arenaria* (Choisy) Steudel (non R. & S. 1819) being illegitimate.

Whether the narrow corolla and the exserted pistil and stamens are enough to separate species is a matter of opinion. If not, *Ipomoea steudelii* would be included in the synonymy of *I. eggersiana* Peter.

House recognized the differences between these plants and described the plant from the Virgin Islands (St. Thomas) under the name *Exogonium eggersii* (1908). However, Peter had already named the species in his treatment of the Convolvulaceae in 1891. Peter's description was quite inadequate, and the species would have been unidentifiable except for the fact that he mentioned the locality and the short shoot, a distinctive character. These shoots are so short and the flowers are so much larger than the leaves that the flowers of one shoot appear to be an inflorescence.

6. **Ipomoea hederifolia** L. Syst. Nat. ed. 10. **2**: 925. 1759.

Ipomoea coccinea sensu auct., non L. 1753.
Ipomoea angulata Lam. Tabl. Encycl. Méth. **1**: 464. 1793.
Ipomoea phoenicea Roxb. Fl. Indica **2**: 92. 1824.
Convolvulus angulatus (Lam.) Sprengel, Syst. Veg. **1**: 596. 1825 [1824].
Convolvulus phoeniceus (Roxb.) Sprengel, *ibid.*
Quamoclit phoenicea (Roxb.) Choisy, Mém. Soc. Hist. Nat. Genève **6**: 433. 1834.
Quamoclit angulata (Lam.) Bojer, Hortus Maurit. 224. 1837.
Quamoclit coccinea sensu Urban, Symb. Antill. **4**: 514. 1910, non Moench, 1794.

COMMON NAMES. Liseron hallier (Guadeloupe); liseron rouge (Martinique).

Herbaceous vine, glabrous or glabrescent. Petioles about equal to the midribs, up to 9 cm. long; blades membranous, apex acuminate, base cordate, the margin simple, angular in the lower half and/or with 2 large basal lobes. Peduncles sturdier and much longer than subtending petioles, bearing few- to several-flowered dichasia; pedicels 1–1.5 cm. long, ribbed, thickening in fruit; sepals rounded at the apex, subequal, ca. 3 mm., with a subulate appendage near the apex, appendages equal to or longer than sepals; corolla scarlet, salver shaped, the tube ca. 3.5 cm., usually slightly curved; stamens and pistil exserted. Capsule globose, 6–8 mm. high, short beaked (1 mm.), 4-valved, 4-celled; seeds 4, covered with short hairs; transparent septae persisting after seeds are shed.

GENERAL DISTRIBUTION. Tropical America; introduced into the Old World tropics.

DISTRIBUTION IN LESSER ANTILLES. St. Barts, St. Kitts, Antigua, Montserrat, Guadeloupe, Dominica, Martinique, Barbados, St. Vincent, Cannouan, Grenada.

This species can be most readily distinguished from the continental species *Ipomoea coccinea* L. by the capsule. In *I. coccinea* the beak is about three times as long, and the pedicel is reflexed instead of upright.

7. **Ipomoea indica** (Burman) Merr. var. **acuminata** (Vahl) Fosberg, Bot. Not. **129**: 38. 1976.

Convolvulus acuminatus Vahl, Symb. Bot. **3**: 26. 1794.
Ipomoea acuminata (Vahl) R. & S. Syst. Veg. **4**: 228. 1819, non Ruiz & Pavon, 1799, an invalid name.
Ipomoea cathartica Poiret in Lam. Encycl. Méth. Bot. Suppl. **4**: 633. 1816.
Pharbitis cathartica (Poiret) Choisy in DC. Prodr. **9**: 342. 1845.
Pharbitis acuminata (Vahl) Choisy in DC. *ibid.*

COMMON NAME. Patate marron (Guadeloupe).

Herbaceous vine of hedges and fields, occasionally rooting along the

stem, not only at nodes, glabrous or occasionally pubescent. Petioles longer or shorter than blades; blades cordate, entire or 3-lobed, middle lobe oblong or elliptic, lateral lobes ovate, midrib up to 10 cm. long, the apex acuminate, mucronate. Peduncles (1- to) several-flowered; inflorescences cymose; bracts membranous, linear, 10–18 mm. long; calyx foliaceous (frequently curling in drying), sepals very unequal in width, the outer 2 ovate, the innermost almost linear, up to 2 cm. long, acuminate; corolla funnel shaped, 6–7 cm. long, deep blue with white center early in the morning, blue portion becoming purple to pink late in the day; ovary surrounded by deep disc. Capsule (2- to) 3-celled, globose, 10–15 mm. wide, beaked, 3- (to 6-)valved; seeds black, smooth, with short hairs around the hilum.

GENERAL DISTRIBUTION. Tropical America.

DISTRIBUTION IN LESSER ANTILLES. St. Kitts, Montserrat, Guadeloupe, St. Vincent.

8. **Ipomoea macrantha** R. & S. Syst. Veg. **4**: 251. 1819.

Ipomoea violacea L. Sp. Pl. 161. 1753, *nomen dubium*; Manitz, Feddes Repert. **88**: 265. 1977.
Convolvulus grandiflora Jacq. Hortus Bot. Vindob. **3**: 39. *pl. 69*. 1776 [1777].
Ipomoea longiflora R. Br. Prodr. 484. 1810, non Willd. 1809.
Convolvulus tuba Schlecht. Linnaea **6**: 735. 1831.
Ipomoea glaberrima Bojer ex Bouton in Hooker, Jour. Bot. Hooker **1**: 357. 1834 [1835].
Calonyction grandiflorum (Jacq.) Choisy, Mém. Soc. Hist. Nat. Genève **6**: 442. 1834, in note.
Calonyction muticum Decaisne, Nouv. Ann. Mus. Paris **3**: 390. 1834.
?*Convolvulus catharticus* Blanco, Fl. Filip. 94. 1837.
Calonyction comosperma Bojer, Hortus Maurit. 228. 1837.
Ipomoea tuba (Schlecht.) G. Don, Gen. Syst. **4**: 271. 1838 [1837?].
Calonyction jacquinii G. Don, *ibid*. 264.
Calonyction tuba (Schlecht.) Colla, Mem. Nuova Sp. Calon. 15. 1840.
Ipomoea grandiflora (Jacq.) Hallier f. Bot. Jahrb. **18**: 153. 1893, nec Lam. 1791, nec Roxb. 1832.
Calonyction album sensu House, Bull. Torrey Bot. Club **31**: 591. 1904, description only, not *I. alba* L.

COMMON NAMES. Sultane grande, belle de nuit, liane blanche bord de mer (Guadeloupe); fleur de nuit, liane douce, liane douce bord de mer (Martinique).

Fleshy, glabrous creeper or climber of coastal areas; older stems straw colored, drying shiny and wrinkled. Petioles up to 11 cm. long; blades with midrib about equal to petiole, base deeply cordate, apex usually acuminate, the margin entire, or occasionally lobed about halfway up each side, each lobe with an acuminate tip. Peduncles usually shorter than subtending petioles; flower(s) 1, occasionally 2; sepals rounded at apex, shortly mucronate, thin on the margins, ca. 2 cm. long, the outer slightly shorter than

the inner; corolla white, the tube 7–8 cm. long, narrow, the limb about as wide as length of tube. Pedicel thickened, becoming longer and more club shaped in fruit; sepals enlarging, becoming fleshy, finally drying and turning back against pedicel; capsule globose, straw colored, 2–3 cm. high, 2-celled, dehiscing into 4 parchment-like valves; seeds 4, brown-black, pubescent, with long, light brown, silky hairs along the margins and around the hilum.

GENERAL DISTRIBUTION. The tropics.

DISTRIBUTION IN LESSER ANTILLES. Saba, St. Eustatius, St. Kitts, Guadeloupe, Martinique, St. Lucia, Barbados, St. Vincent, Bequia, Prune Island.

As stated in an earlier paper (Powell, Nicolson, & Austin, 1978, p. 202), we agree that the lectotype of *Ipomoea violacea* L. is the Boerhaave copy of a Plumier drawing most probably to be identified with *I. macrantha*. However, before accepting *I. violacea* as the correct name, we prefer to wait until the original Plumier drawing is studied.

9. **Ipomoea mauritiana** Jacq. Collect. **4:** 216. 1791.

Convolvulus paniculatus L. Sp. Pl. **1:** 156. 1753.
Ipomoea gossypifolia Willd. Enum. Pl. 208. 1809.
Ipomoea paniculata (L.) R. Br. Prodr. 486. 1810, non Burman f. 1768.
Ipomoea insignis Andrews, Bot. Repos. **10:** *pl. 636.* 1797 [1811].
Ipomoea ennealoba Beauv. Fl. Oware Bénin Afr. **2:** 69. *t. 101.* 1818.
Ipomoea eriosperma Beauv. *ibid.* 73. *t. 105.*
Convolvulus roseus H.B.K. Nov. Gen. Sp. **3:** 108 (84 in folio ed.). 1818 [Feb. 1819].
Ipomoea quinqueloba Willd. ex R. & S. Syst. Veg. **4:** 789. (Jan.–June) 1819.
Convolvulus insignis (Andrew) Sprengel, Syst. Veg. **1:** 592. 1824.
Batatas paniculata (L.) Choisy, Mém. Soc. Hist. Nat. Genève **6:** 436. 1834.
Ipomoea digitata sensu auct., non L. 1759; Griseb. Fl. Brit. W. Indian Is. 469. 1862.

Heavy vine with tuberous roots. Petioles shorter than blades, usually with minute hairs, top glandular; blades up to 15 cm. across, 10 cm. long, veins usually with minute hairs, usually deeply palmatifid with 7, 5, or 3 lobes, the lobes oblong-lanceolate, entire, the basal ones sometimes ovate. Peduncles longer and stouter than petioles; flowers many to few, crowded; buds rounded; sepals glabrous, rounded at the apex, concave, ca. 8 mm. long, coriaceous; corolla pink, lilac, sometimes darker, ca. 5 cm. long. Capsule globose, ca. 1 cm. in diameter, basal portion cupped by calyx, splitting by 4 valves, 2-celled; seeds 4, with long hairs.

GENERAL DISTRIBUTION. The tropics.

DISTRIBUTION IN LESSER ANTILLES. Martinique, Barbados, St. Vincent.

10. **Ipomoea nil** (L.) Roth, Catalecta Bot. **1:** 36. 1797.

Convolvulus nil L. Sp. Pl. ed. 2. **1:** 219. 1762.
Convolvulus hederaceus L. *ibid.*

Ipomoea scabra Forskål, Fl. Aegypt.-Arab. 44. 1775.
Ipomoea cuspidata Ruiz & Pavon, Fl. Peruv. Chil. **2:** 11. *t. 119, fig. a.* 1799.
Ipomoea setosa Blume, Bijdr. Fl. Ned. Indië, 714. 1825 [1826].
Convolvulus tomentosus Vell. Fl. Flum. **1:** 74. 1825; *ibid.*, Icones **2:** *t. 65.* 1827.
Pharbitis nil (L.) Choisy, Mém. Soc. Hist. Nat. Genève **6:** 439. 1834.
Pharbitis cuspidata (Ruiz & Pavon) G. Don, Gen. Syst. **4:** 263. 1838 [1837?].
Ipomoea trichocalyx Steudel, Nom. Bot. ed. 2. **1:** 819. 1840, non G. Don, 1838 [1837?].
Ipomoea longicuspis Meissner in Martius, Fl. Brasil. **7:** 227. 1869.

COMMON NAMES. Liseron hallier, liseron bleu (Guadeloupe); liseron bleu (Martinique).

Herbaceous twiner; stems, petioles, and peduncles usually retrorsely pilose. Leaves entire to deeply 3-lobed, midrib up to 12 cm. long, pilose to glabrescent on both surfaces, blunt to acuminate at tips of lobes, the base cordate, the apex acuminate. Peduncles 1–16 cm. long; flowers (1 to) several; bracts linear, the lowest 8–10 mm. long; sepals 2–3 cm. long, broader, covered with long, patent hairs at the base, the upper portion upright, long and narrow, scarcely tapering; corolla funnel shaped, 3–5 cm. long, blue with a white tube. Sepals widening at base and surrounding the globose, 3-celled, 3-valved capsule; seeds 6 or fewer, brown-black, covered with short hairs.

GENERAL DISTRIBUTION. Throughout the tropics; often cultivated.

DISTRIBUTION IN LESSER ANTILLES. St. Martin, St. Barts, Saba, St. Eustatius, Antigua, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Ronde, Grenada.

11. Ipomoea obscura (L.) Ker-Gawler, Bot. Reg. 3: *t. 239.* 1817.

Convolvulus obscurus L. Sp. Pl. ed. 2. **1:** 220. 1762.
Ipomoea solanifolia Burman f. Fl. Indica, 49. 1768, non L. 1753.
Ipomoea luteola R. Br. Prodr. 485. 1810.
Ipomoea insuavis Blume, Catal. 50. 1823.

Slender vine. Petioles usually slightly shorter than blades; blades entire, cordate, varying in size to ca. 8 cm. from base of basal lobe to apex, glabrous, sometimes ciliate, or more often hairy on one or both surfaces. Peduncles longer and more slender than subtending petioles, bearing 1 to 3 flowers; bracts 2, minute; buds pointed; sepals glabrous to pubescent, acute, subequal, 3–4 mm. long; corolla white or cream, dark centered, funnel shaped, 2–2.5 cm. long. Capsule straw colored, globose, ca. 1 cm. high, 2-celled, 4-valved; seeds 4, black, completely covered by short hairs.

GENERAL DISTRIBUTION. Eastern tropical Africa to Fiji, Polynesia, West Indies.

DISTRIBUTION IN LESSER ANTILLES. Antigua, Marie Galante, Barbados.

12. **Ipomoea pes-caprae** (L.) R. Br. subsp. **brasiliensis** (L.) Ooststr. Blumea 3: 533. 1940.

Convolvulus brasiliensis L. Sp. Pl. 1: 159. 1753.
Ipomoea pes-caprae sensu R. Br. in Tuckey, Narr. Exped. Zaire, 477. (March) 1818, non *Convolvulus pes-caprae* L. Sp. Pl. 1: 159. 1753.
Convolvulus maritimus Desr. in Lam. Encycl. Méth. Bot. 3: 550. 1792.
Ipomoea crassifolia Pers. Syn. Pl. 1: 184. 1805.
Ipomoea maritima (Desr.) R. Br. Prodr. 486. 1810.
Ipomoea orbicularis Elliott, Bot. S. Carolina Georgia 1: 257. 1817.
Ipomoea brasiliensis (L.) Sweet, Hortus Suburban London, 35. June/July, 1818.
Ipomoea brasiliensis (L.) G. F. W. Meyer, Primitiae Florae Essequeboensis, 97. Nov. 1818.
Convolvulus bilobatus Roxb. Fl. Indica 2: 73. 1824.
Convolvulus rotundifolius Schum. & Thonn. Beskr. Guineiske Pl. 102. 1827.
Ipomoea pes-caprae (L.) R. Br. var. *emarginata* Hallier f. Bull. Soc. Bot. Belg. 37: 98. 1898.

COMMON NAMES. Brievengat, ivy, sea vine (Dutch islands); patate bord de mer (Guadeloupe, Martinique); passe-pierre (les Saintes); seaside-yam, goat's foot, ipomoea (Barbados).

Prostrate seashore plant, glabrous; stems with latex. Petioles 1–12 cm. long; blades oblong to rotund, emarginate to shallowly bilobed, up to 12 cm. long, subcoriaceous, with a gland on either side of the midrib on the under surface at the base of the blade, apex mucronate, base truncate to cuneate. Peduncles shorter or longer than subtending petioles; flowers (1 to) several; bracts small; pedicel(s) 2–5 cm. long; sepals rounded at the apex, mucronate, the outer 2 shorter, the inner ones ca. 1 cm. long; corolla funnel shaped, dark lavender, ca. 5–6 cm. deep. Capsule globose, lower portion surrounded by persistent calyx, dehiscing into 4 valves, brown on the outside, very light brown to white on the inside, 2-celled; seeds 4, covered with dark brown hairs.

GENERAL DISTRIBUTION. Tropical seashores.

DISTRIBUTION IN LESSER ANTILLES. St. Martin, St. Barts, St. Eustatius, Antigua, Montserrat, Guadeloupe, La Désirade, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Bequia, Grenada.

13. **Ipomoea phyllomega** (Vell.) House, Ann. N. Y. Acad. 18: 246. 1908 (as *phillomega*).

Convolvulus phyllomega Vell. Fl. Flum. 1: 74. 1825 (as *philomega*); *ibid.*, Icones 2: *pl. 63.* 1827 (as *phillomega*).
Ipomoea capparoides Choisy, Mém. Soc. Hist. Nat. Genève 8: 59. 1839.
Ipomoea demerariana sensu auct., non Choisy, 1845; Griseb. Fl. Brit. W. Indian Is. 471. 1861.
Aniseia syringifolia Dammer, Bot. Jahrb. 23(57): 38. 1897.

COMMON NAME. Patate marron (Martinique).

High-climbing forest twiner with large, cordate leaves. Petioles half the length of midribs or less; blades up to 21 cm. wide, midrib up to 19 cm. long. Peduncles stout, widely branched to form a large, lax corymb; bracts lanceolate, 1–1.5 cm. long, caducous; 2 outer sepals 1.5–2 cm. long, blunt or rounded at the apex, tinged the color of the corolla, more or less surrounding the 3 inner, considerably smaller sepals; corolla campanulate, magenta or deep rose, the tube wide, ca. 4 cm. deep, the limb ca. 6 cm. in diameter. Capsule beaked, globose, 4-valved, 2-celled, surrounded by sepals; seeds 4, pubescent, with long, marginal, brown, silky hairs persistent on the end opposite the hilum.

GENERAL DISTRIBUTION. Central and South America, West Indies.

DISTRIBUTION IN LESSER ANTILLES. St. Kitts, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent.

14. **Ipomoea quamoclit** L. Sp. Pl. 1: 159. 1753.

Convolvulus pennatus Desr. in Lam. Encycl. Méth. Bot. **3:** 567. 1792.
Convolvulus quamoclit (L.) Sprengel, Syst. Veg. **1:** 591. 1824.
Quamoclit vulgaris Choisy, Mém. Soc. Hist. Nat. Genève **6:** 434. 1833.
Quamoclit pinnata Bojer, Hortus Maurit. 224. 1837.
Quamoclit quamoclit (L.) Britton in Britton & Brown, Illus. Fl. No. U. S. **3:** 22. 1898.

COMMON NAMES. Regadero, sweet Willy (Dutch islands); cheveux de Vénus, liane rouge, herbe à éternuer, goutte de sang (Guadeloupe); cheveux de Vénus, lin (Martinique); sweet William (St. Vincent, Barbados).

Slender, glabrous, herbaceous twiner. Petioles less than 1 cm. to as long as leaf blades, up to 6 cm. long; blades ovate, very deeply pinnately partite, segments linear, the apical segment usually mucronate, the basal pair subdivided; leaves of axillary buds appearing like stipules. Peduncles usually longer than subtending petioles, bearing 1 to few scarlet or occasionally white (Guadeloupe) flowers; bracts small; sepals unequal, rounded at the apex, mucronate, the longest (inner) ca. 5–6 mm. long; corolla salver shaped, the tube 2–2.5 cm. long, the limb 5-lobed, ca. 2 cm. across; stamens and pistil exserted, entire pistil often persisting until capsule matures. Capsule ovoid, lower portion surrounded by persistent calyx, straw colored, 4-valved, 4-celled; seeds 4, ovate, black with minute, brown hairs; septae persistent, transparent with brown margins.

GENERAL DISTRIBUTION. Of uncertain origin; widespread in the tropics; usually cultivated.

DISTRIBUTION IN LESSER ANTILLES. St. Martin (*fide* Broeders), St. Barts, Saba, St. Eustatius, St. Kitts, Antigua, Guadeloupe, Marie Galante, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Grenada, Cannouan.

In the Lesser Antilles it is usually cultivated, but frequently escapes.

15. **Ipomoea repanda** Jacq. Enum. Syst. Pl. 13. 1760 (as *Ipomaea*).

Convolvulus repandus (Jacq.) Desr. in Lam. Encycl. Méth. Bot. 3: 555. 1792.
Exogonium repandum (Jacq.) Choisy, Mém. Soc. Hist. Nat. Genève 8: 50. 1837.
?*Ipomoea eriosperma* Bertero ex Choisy in DC. Prodr. 9: 388. 1845.
Quamoclit repanda (Jacq.) G. Roberty, Candollea 14: 41. 1952.

COMMON NAMES. Liane patate, patate grand bois, patate rouge bord de mer (Guadeloupe); capi (Dominica); fleur rouge bois, patate grand bois (Martinique).

High climbing, glabrous twiner with tuberous roots. Petioles about half as long as leaf blades; blades ovate to cordate, up to 11 cm. long and 7 cm. wide, somewhat coriaceous, base truncate or cordate, apex obtuse or acuminate and mucronate, margins usually entire, occasionally 1 or 2 long, narrow lobes on either side at the base, the center lobe narrow, gradually tapering to the apex. Peduncles stouter and longer than subtending petioles; inflorescences with (1 to) several flowers in lax compound umbels tending to branch dichotomously; bracts linear, caducous; sepals subequal, ca. 6–7 mm. long, rounded, tinged the color of the corolla; corolla bright pink to cerise, the tube ca. 3 cm. long, curved, the limb completely lobed, reflexed, lobes 1.5–2 cm. long; stamens and pistil exserted. Capsule brown, ovoid, 10–12 mm. high, beaked, sitting in calyx, 4-valved, the valves lighter on the inside, 2-celled; seeds 4, black, with 2 rows of long, silky, brown hairs.

This description represents *Ipomoea repanda* var. *repanda*, found in the Lesser Antilles.

GENERAL DISTRIBUTION. Puerto Rico, Lesser Antilles.

DISTRIBUTION IN LESSER ANTILLES. Barbuda, Antigua, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Bequia, Grenada.

It should be noted that in Puerto Rican specimens the leaves are narrower and the pedicels widen more gradually into the calyx.

Ipomoea repanda var. **microdactyla** (Grisebach) Powell, stat. nov.

Ipomoea microdactyla Grisebach, Cat. Pl. Cubens. 204. 1866.

This variety is native to Florida, the Bahamas, and Cuba. The change of status better reflects its close relationship with *Ipomoea repanda* var. *repanda* of the eastern Caribbean islands. Their flowers, inflorescences, and fruits are the same, except that in var. *microdactyla* the inflorescence is smaller, and the corolla shows more variation in the depth of lobing, sometimes showing almost none. The leaves of var. *microdactyla* are also more variable, ranging from entire to very deeply 5-lobed. Perhaps the fact that *I. repanda* var. *microdactyla* is considerably smaller than the other variety is partly due to habitat: var. *microdactyla* grows in sandy soils, while var. *repanda* is a high climber that often grows in forests.

16. **Ipomoea setifera** Poiret in Lam. Encycl. Méth. Bot. **6**: 17. 1804.

Convolvulus ruber Vahl, Eclog. **2**: 12. 1798.
Ipomoea breviflora G. F. W. Meyer, Primitiae Florae Essequeboensis, 100. 1818.
Convolvulus setifer (Poiret) Sprengel, Syst. Veg. **1**: 597. 1825 [1824].
Calystegia setifera (Poiret) Meissner in Martius, Fl. Brasil. **7**: 316. 1869.
Ipomoea lesteri Baker, Kew Bull. **64**: 83. 1892.
Ipomoea assumptionis Britton, Ann. N. Y. Acad. **7**(11): 170. 1893.
Ipomoea ruber (Vahl) Millsp. Field Mus. Publ. Bot. Ser. **2**: 86. 1900, non *I. rubra* Murray, 1774.
Ipomoea ruber (Vahl) Millsp. var. *albo-flavida* Urban, Symb. Antill. **3**: 345. 1902 (as *rubra*).
Ipomoea ruber (Vahl) Millsp. var. *palustris* Urban, *ibid.* (as *rubra*).
Ipomoea palustris Urban, *ibid.* **9**: 423. 1925.

COMMON NAMES. Liane à faux, liane douce (Guadeloupe); coudrel (Martinique).

Trailing or twining herbaceous vine; stems with or without long, stiff, yellow hairs. Petioles shorter or longer than blades, sometimes tuberculate; blades usually sagittate with rounded lower lobes and blunt, mucronate apical lobe, sometimes cordate with entire margin, glabrous, the midrib up to 11 cm. long, with or without hairs. Peduncles thicker, shorter or longer than subtending petioles, bearing 2 large, boat-shaped, acuminate bracts; bracts 1.5–2 cm. long, surrounding an inflorescence of 1 to several flowers, each flower with a pair of bracts that persist until flower matures; pedicels 1–2 cm.; sepals unequal, caudate-acuminate, the outer ones ca. 2 cm. long, with prominent longitudinal veins, winged at the base, keels becoming more prominent and sometimes muricate with maturity; corolla rose colored, funnel shaped, 7–9 cm. long, the limb 5-pointed. Calyx surrounding and extending beyond capsule; capsule 4-valved, 2-celled; seeds 4, gray-brown, tomentose.

GENERAL DISTRIBUTION. Central America, tropical South America, West Indies, tropical Africa.

DISTRIBUTION IN LESSER ANTILLES. Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent.

17. **Ipomoea sphenophylla** Urban, Symb. Antill. **5**: 474. 1908.

Glabrous climber. Petioles (10–)15 mm. long; blades (3–)7 cm. long and (1–)2 cm. wide, entire, oblanceolate or obtriangular, gradually sloping to the base, the apex truncate and retuse, mucronate. Peduncles 2–3 cm. long; inflorescence several- to many-flowered; pedicels (2–)3 cm. long; sepals 5–7 mm. long, subequal, chartaceous, apex rounded; corolla unknown. Capsule globose, 6–7 mm. in diameter, 4-valved(?); seeds 4 mm. long, dark brown, with long, light brown, woolly hairs on the margins.

GENERAL DISTRIBUTION. Endemic to St. Eustatius.

Only two collections of this plant have been recorded (both from Signal Hill), neither of which has been seen by this writer.

18. **Ipomoea stolonifera** (Cyr.) J. F. Gmelin, Syst. Nat. ed. 13. 2: 345. 1791.

Convolvulus stoloniferus Cyr. Pl. Rar. Regni Neapol. **1:** 14. *t. 5.* 1788.
Convolvulus littoralis L. Syst. Nat. ed. 10. 924. 1759.
Convolvulus arenarius Vahl, Symb. Bot. **1:** 18. 1790.
Convolvulus repens Sw. Obs. Bot. 64. 1791.
Convolvulus acetosaefolius Vahl, Eclog. **1:** 18. 1796 [1797].
Ipomoea stolonifera (Cyr.) Poiret in Lam. Encycl. Méth. Bot. **6:** 20. 1804.
Ipomoea carnosa R. Br. Prodr. 485. 1810.
Ipomoea acetosaefolia (Vahl) R. & S. Syst. Veg. **4:** 246. 1819.
Ipomoea arenaria (Vahl) R. & S. *ibid.* 247.
Ipomoea littoralis (L.) Boiss. Fl. Orient. **4:** 112. 1875, non Blume, 1825.

COMMON NAME. Liseron blanc (Guadeloupe).

Seashore plant with wrinkled stems creeping in sand, rooting at nodes, occasionally climbing bushes; glabrous, a few patent hairs occasionally at nodes or tops of petioles. Petioles 0.5–10 cm. long; blades somewhat thick, usually simple, oblong, 2–13 cm. long, 0.5–4 cm. wide, usually twice as long as wide, the apex emarginate, mucronate, the base shortly attenuate but varying to cordate, hastate, or even lobed. Peduncles usually as long as petioles, bearing 1 (to 3) flowers; pedicels stouter and longer; bracts small; sepals equal or with 2 outer ones shorter, oblong with mucronate apex, ca. 15 mm. long in flower, becoming somewhat larger and usually purplish or purple spotted in fruit; corolla white, 4–5 cm. long. Capsule globose to conical depending on number of seeds, 4-celled, 4-valved; seeds (1–)4, with woolly hairs.

GENERAL DISTRIBUTION. Circumtropical.

DISTRIBUTION IN LESSER ANTILLES. Guadeloupe, Martinique, St. Lucia, St. Vincent.

19. **Ipomoea tiliacea** (Willd.) Choisy in DC. Prodr. **9:** 375. 1845.

Convolvulus tiliaceus Willd. Enum. Pl. **1:** 203. 1809.
Convolvulus fastigiatus Roxb. Hortus Bengal. 13. 1814, *nomen nudum.*
Ipomoea cymosa G. F. W. Meyer, Primitiae Florae Essequeboensis, 99. 1818.
Convolvulus essequebensis Sprengel, Syst. Veg. **1:** 600. 1824.
Ipomoea fastigiata (Roxb.) Sweet, Hortus Brit. 288. 1827.
Ipomoea surinamensis Miq. Linnaea **18:** 600. 1845.
Ipomoea alba Garcke, Linnaea **22:** 66. 1848, non L. 1753.
Ipomoea longipes Garcke, *ibid.*
Ipomoea stenocolpa Garcke, *ibid.* 67.
Ipomoea batatas (L.) Lam. var. *fastigiata* Kuntze, Rev. Gen. Pl. **2:** 442. 1891.
Ipomoea gracilis sensu auct., non R. Br.; House, Ann. N. Y. Acad. **18:** 248. 1908.

COMMON NAMES. Wild potato vine (Dutch islands); liane douce, patate marron, patate bâtard, patate à cochon, patate sauvage (Guadeloupe); liane douce, patate sauvage (Martinique); wild slip, wild potato (Barbados).

Glabrous climber with slender stems, the older stems becoming striate, twisted, gray, and wiry on drying; roots sometimes tuberous. Petioles slender, about as long as blades; blades cordate or sagittate, occasionally dentate or lobed at the base; the midrib up to 14 cm. long, usually shorter, the petiole and veins sometimes red, the apex acuminate and mucronate, the base deeply cordate. Peduncles usually stouter and longer than subtending petioles; bracts small and caducous; inflorescence fastigiate; flowers few to many, sepals ca. 1 cm. long, with long, pointed apices very conspicuous in crowded, long and narrow buds, widening in flower, the inner ones much wider, all retaining the acuminate tips; corolla funnel shaped, pale lilac with dark purple center, 4–5 cm. long; anthers bearing microscopic glandular papillae. Capsule depressed-globose, beaked, brown, 2-celled, 4-valved, with sepals reflexed against pedicel; seeds 4 or fewer, smooth, brown-black; septum persistent.

GENERAL DISTRIBUTION. Tropical America, Polynesia, introduced in Old World tropics.

DISTRIBUTION IN LESSER ANTILLES. St. Martin, Saba, St. Eustatius, St. Kitts, Antigua, Montserrat, Guadeloupe, Marie Galante, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Bequia, Grenada.

This species, with conspicuous flowers, is a climber on trees and shrubs. According to Duss (Ann. Inst. Colon. Marseille 3: 437. 1897), it bears tuberous roots that are edible but that do not have the flavor of the sweet potato, *I. batatas*. The two species are so closely related that it is sometimes extremely difficult to determine herbarium material. The sweet potato is cultivated throughout the tropics; its stout, succulent stems run along the ground, sending down frequent roots which produce palatable storage organs, the tips of the stem turning upward. *Ipomoea batatas* also differs from *I. tiliacea* in sometimes being quite hairy and in frequently having palmately divided leaves. Its inflorescence is less conspicuous, smaller, more umbellate, and with coarser pedicels; herbarium material rarely has fruits, either because the plant rarely sets fruit, or because it seldom gets a chance to, the roots being harvested first. The ovaries and fruits usually have long, stiff hairs.

20. **Ipomoea tricolor** Cav. Ic. Descr. Pl. 3: 208. *t. 5*. 1795.

Ipomoea rubro-caerulea Hooker, Bot. Mag. **61:** *t. 3297*. 1834.
Convolvulus rubro-caeruleus (Hooker) Dietr. Synopsis Pl. **1:** 670. 1839.
Ipomoea puncticulata Bentham, Bot. Voy. Sulphur, 136. 1845.
Pharbitis rubro-coerulea (Hooker) Planchon, Fl. Serres **9:** 281. *t. 966*. 1854.
Ipomoea violacea sensu auct., non L. 1753; Griseb. Fl. Brit. W. Indian Is. 469. 1862.

COMMON NAME. Liane douce (Guadeloupe).

Glabrous climber. Petioles shorter than, to twice the length of, blades; blades cordate, up to 14 cm. wide, basal sinus 2–3 cm. deep, midrib up to 12 cm. long, the apex pointed, mucronate. Peduncles usually longer and stouter than subtending petioles, producing few to several flowers; bracts minute; pedicels 2–3 cm. long; sepals equal, 3–5 mm. long, triangular, acute, green with white edge; corolla blue, funnel shaped, up to 7 cm. long. Capsule conical, ca. 1 cm. tall not including the long beak that falls off at dehiscence, 2-celled, 4-valved; seeds 4, black, pilose.

GENERAL DISTRIBUTION. Tropical America; and widely cultivated.

DISTRIBUTION IN LESSER ANTILLES. St. Martin, Saba, Antigua, Guadeloupe.

See *Ipomoea macrantha* for note on *I. violacea*.

21. **Ipomoea triloba** L. Sp. Pl. 1: 161. 1753.

Ipomoea eustachiana Jacq. Obs. Bot. 2: 12. *t. 36.* 1767.
Ipomoea parviflora Vahl, Symb. Bot. 3: 34. 1794.
Convolvulus sloanei Sprengel, Syst. Veg. 1: 593. 1824.

COMMON NAMES. Liane purgative, petite patate marron (Guadeloupe, Martinique); petite liane douce (Martinique).

Light creeper or climber, glabrous or with few hairs on stems and leaves. Leaves deeply 3- (to 5-)lobed, main midrib 2–4 cm., middle lobe lanceolate or ovate, lower lobes deltoid or lobed; occasionally leaf entire. Peduncles stouter and sometimes longer than subtending petioles, bearing 1 to several flowers; pedicels often tubercled; sepals ca. 5 mm. long, unequal, acute, mucronate, ciliate and/or hirsute, especially below; corolla pink-purple, 2–3 cm. long, funnel shaped. Capsule globose, surrounded by enlarged calyx, ca. 5 mm. high, hirsute above, 4-valved, 2-celled; seeds 4, dark brown, smooth.

GENERAL DISTRIBUTION. Originating in tropical America; now widespread as a tropical weed.

DISTRIBUTION IN LESSER ANTILLES. St. Barts, St. Eustatius, St. Kitts, Antigua, Guadeloupe, Martinique, Barbados.

One specimen examined (*Stehlé 3674* (GH, US)) has particularly large sepals for this species, but without flowers it is unwise to presume that this is *Ipomoea trichocarpa* Ell. or any other related species that would be a new record for Martinique and the Lesser Antilles.

22. **Ipomoea turbinata** Lagasca, Gen. Sp. Nov. 10. 1816.

Convolvulus muricatus L. Mant. Syst. Veg. 44. 1767.
Ipomoea muricata (L.) Jacq. Pl. Rar. Horti Caes. Schoenbr. 3: 40. *t. 323.* 1798 [1803?], non Cav. 1799.

Ipomoea bona-nox L. var. *purpurascens* Ker-Gawler, Bot. Reg. **4**: *t. 290.* 1818.
Calonyction muricatum (L.) G. Don, Gen. Syst. **4**: 264. 1838 [1837?].
Calonyction longiflorum Hassk. Pl. Javan. Rar. 523. 1848.
Calonyction speciosum Choisy var. *muricatum* (L.) Choisy in DC. Prodr. **9**: 345. 1845.
?*Convolvulus colubrinus* Blanco, Fl. Filip. ed. 2. 66. 1845.
Calonyction speciosum sensu Boldingh, Fl. Dutch W. Indian Is. 163. 1909, non Choisy, 1834.

COMMON NAME. Lilac bell (St. Eustatius).

Well-branched, glabrous vine with recurved prickles or warts on stems and often on peduncles, sometimes on petioles. Petioles shorter or longer than midribs, up to 10 cm. or more; blades entire or 3-lobed, apex acuminate and mucronate, base deeply cordate. Peduncles heavier and usually shorter than subtending petioles; flowers 1 to few; bracts small, falling very early; pedicel(s) thickened above; sepals ca. 1 cm. long, unequal, keeled on the midrib, awned, the awns usually flaring outward; corolla 5–8 cm. long, funnel shaped, with a narrow tube, lilac to purple, open at night, closing early in the day; stamens and pistil scarcely exserted. Pedicel thickening and becoming retrorse in fruit; capsule conical, 1.5–2 cm. high, beaked, dehiscent, 4-valved, 2-celled; seeds 4, brown, smooth.

GENERAL DISTRIBUTION. The tropics; sometimes cultivated.

DISTRIBUTION IN LESSER ANTILLES. St. Eustatius.

23. **Ipomoea walpersiana** Duchassaing ex Urban, Symb. Antill. 3: 345. 1902.

Glabrous vine; stems more or less 3- or 4-angular. Petioles 4–9 cm. long; lower leaves triangular with subtruncate base, 7–9 cm. broad, 6–8 cm. long, apex acuminate; upper leaves narrowly ovate or ovate-triangular, gradually narrowing to apex, base broadly cordate, lobes spreading, 3.5–5 cm. broad, 5–7 cm. long, margin entire. Peduncles 3–15 cm. long; corymbs several- to many-flowered; pedicels 15–20 mm. long; bracts ovate, (1–)1.5 mm. long; sepals glabrous, very unequal, outer ones 4–6 mm. long, inner ones 7.5–8 mm. long, all apices rounded; corolla purple, 5 cm. long, narrowly funnel shaped, 8 mm. wide above the middle (herbarium material); ovary 2-celled, ovules 4. Capsule globose, 10–12 mm. in diameter, 4-valved; seeds brown-black, velvety, with long, patent, white hairs on the margin except at the base.

GENERAL DISTRIBUTION. Endemic to Guadeloupe.

The above information was taken from the original description and from Fournet (1978). Only two collections of this species have been recorded.

24. **Ipomoea wrightii** Gray, Synopt. Fl. N. A. II. 1: 213. 1878.

Ipomoea pulchella sensu auct., non Roth, 1821; Griseb. Fl. Brit. W. Indian Is. 470. 1862.

Convolvulus heptaphylla Roxb. Fl. Indica **2:** 66. 1824, non Rottler & Willd. 1803.
Ipomoea heptaphylla sensu auct., non Voigt, 1845; Britton & Wilson, Sci. Survey Porto Rico Virgin Is. **6:** 114. 1925.
Ipomoea spiralis House, Muhlenbergia **3:** 40. 1907 (as *spirale*).

COMMON NAME. Patate marron (Guadeloupe).

Slender twiner, almost completely glabrous. Leaves palmately compound, petioles longer than leaf blades; leaflets 5, membranous, one or more frequently lobed, middle one not usually conspicuously longer than others, leaflets and lobes lanceolate to ovate, obtuse or acute, each with apex usually mucronate and base cuneate. Peduncles filiform and wavy, shorter than the subtending petioles, twisting to place the flower beyond the shadow of the blade, occasionally tomentose toward the upper end; bracts very small; pedicels much shorter and sturdier than peduncles, ca. 1 cm. long; calyx shorter than pedicel, the sepals rounded, accrescent, turning completely backward as fruit matures; corolla lilac, ca. 2 cm. long. Capsule globose, 2-celled, splitting irregularly, exposing the persistent, transparent septum; seeds 4 or fewer, with long, cottony hairs, clinging to the remains of the fruit for an indefinite period.

GENERAL DISTRIBUTION. Tropical America.

DISTRIBUTION IN LESSER ANTILLES. Antigua, Guadeloupe, Barbados.

One specimen examined had more than one flower per peduncle.

This plant species, with the distinctive spiraling of its filiform peduncle, is not to be confused with *Merremia quinquefolia*, which it resembles. It seems to have been the plant that appeared spontaneously in the Calcutta garden and that was described under the name of *Convolvulus heptaphylla* by Roxburgh.

9. **Stictocardia** Hallier f. Bot. Jahrb. **18:** 159. 1893.

Climbers, usually pubescent. Leaves ovate to orbicular, with minute glands on the lower surface of the blade, margin entire. Peduncles axillary, bearing 1 to many flowers; bracts small, caducous; sepals more or less equal, rounded at the apex; corolla large, funnel shaped, pink, red, or purple; stamens and pistil included; pollen spiny. Calyx becoming much enlarged and coarse in fruit, completely surrounding the indehiscent, 4-celled fruit; seeds 4, brown, pubescent, freed by disintegration of calyx and pericarp.

TYPE SPECIES: *Stictocardia tiliifolia* (Desr.) Hallier f.

Stictocardia tiliifolia (Desr.) Hallier f. Bot. Jahrb. **18:** 159. 1893 (as *tiliaefolia*).

Convolvulus tiliaefolius Desr. in Lam. Encycl. Méth. Bot. **3:** 544. 1792.
Ipomoea tiliaefolia (Desr.) R. & S. Syst. Veg. **4:** 229. 1819.
Convolvulus gangeticus Roxb. Fl. Indica **2:** 46. 1824.

Ipomoea pulchra Blume, Bijdr. Fl. Ned. Indië, 716. 1826.
Rivea tiliaefolia (Desr.) Choisy, Mém. Soc. Hist. Nat. Genève **6**: 407. 1834.
Argyreia tiliaefolia (Desr.) Wight, Ic. Pl. Indiae Orient. **4**(2): 12 (as *tillaefolia*). *t. 1358* (as *tilifolia*). 1848.
Rivea campanulata sensu House, Muhlenbergia **5**: 72. 1909.
Strictocardia campanulata sensu Merr. Philip. Jour. Sci. Bot. **9**: 133. 1914.
Argyreia campanulata sensu Alston in Trimen, Handb. Fl. Ceylon, Suppl. 201. 1931.

COMMON NAMES. Liane gros boudin, liane gros marron, bois-patate marron (Guadeloupe); gros boudin, liane d'argent bâtard (Martinique).

Stout climber, pubescent or glabrous. Petioles usually longer than blades; blades large, ovate to orbicular, lower surface covered with numerous black or brown dots (sometimes hidden by pubescence), pubescent at least along veins, midrib up to 17 cm. long, apex rounded to acuminate, base cordate but usually slightly cuneate within basal sinus, margin entire. Peduncles shorter than subtending petioles, bearing 1 or occasionally more flowers; sepals ca. 1.5 cm. long, unequal in width, the outer 2 surrounding the others, all rounded, subcoriaceous, with thin edges, pubescent or glabrous, with glands as on the lower surface of the leaf; corolla rose colored with purple center, funnel shaped, ca. 9 cm. long, portions exposed in bud bearing glands and having hairs at tips. Capsule ca. 2 cm. high, 4-celled, brown, beaked, chartaceous, indehiscent, surrounded by the coarser, much enlarged, spongy, conspicuously nerved sepals; seeds 4, brown, pubescent.

GENERAL DISTRIBUTION. The tropics.

DISTRIBUTION IN LESSER ANTILLES. St. Eustatius, Antigua, Montserrat, Guadeloupe, Marie Galante, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Grenada.

The Linnaean species *Ipomoea campanulata* based on "Adamboe" illustrated in Rheede tot Draakestein's *Hortus Indicus Malabaricus* (**11**: 115. *t. 56*. 1692) has often been confused with this *Stictocardia*, but the illustration shows a plant in which the flowers are not usually solitary, the corolla is lobed, the venation is of a different pattern, and the fruit appears to be dehiscent.

10. **Turbina** Rafinesque, Fl. Tellur. **4**: 81. 1838.

Climbers, glabrous or pubescent; leaves cordate with margins entire. Peduncles axillary; corolla funnel or salver shaped; pollen spiny; stigma biglobose, style 1, ovary bilocular, ovules 4. Capsule ellipsoid, circumscissile at the base, with sepals spreading at maturity, 1 seed usually developing.

TYPE SPECIES: *Turbina corymbosa* (L.) Raf.

Turbina corymbosa (L.) Raf. Fl. Tellur. **4**: 81. 1838.

Convolvulus corymbosus L. Syst. Nat. ed. 10. 923. 1759.
Convolvulus domingensis Desr. in Lam. Encycl. Méth. Bot. **3**: 554. 1792.

Convolvulus sidaefolius H.B.K. Nov. Gen. Sp. **3:** 99 (78 in folio ed.). 1818 [1819].
Ipomoea sidaefolia (H.B.K.) Choisy, Mém. Soc. Hist. Nat. Genève **6:** 459. 1834.
Ipomoea burmanni Choisy in DC. Prodr. **9:** 350. 1845.
Rivea corymbosa (L.) Hallier f. Bot. Jahrb. **18:** 157. 1893.
Ipomoea antillana Millsp. Field Mus. Publ. Bot. Ser. **2:** 84. 1900.
Ipomoea domingensis (Desr.) House, Muhlenbergia **3:** 38. 1907.
Legendrea corymbosa (L.) Ooststr. Blumea **5:** 355. 1943.

COMMON NAME. Christmas wreath (Barbados).

Perennial climber, mainly on low bushes, glabrous or minutely pubescent; stems green and terete when young, becoming gray and tending to have flattened sides with age. Petioles slender, usually shorter than blades; blades cordate, often gland-dotted, midrib up to 8 cm. long, apex obtuse to acuminate, margin entire. Peduncles axillary, borne on main stem and secund on short branches; inflorescences cymose, more or less corymbose; bracts small, caducous; young buds conical; sepals arising sharply from flattened base, elliptic, mucronate, green and thickened at base, thickness decreasing toward the apex, margins scarious, the outer 2 much shorter, the inner 3 ca. 1 cm. long; corolla white with dark red or purple center, 2.5–3 cm. long, funnel shaped; pollen very fine; ovary 2-celled, ovules 4. Capsule 8–10 mm. long, brown, smooth, thin walled, ellipsoid, beaked by thickened style base topped by short filamentous portion, sitting in distinct disc; seed(s) 1 (or 2), brown, pubescent; septum pushed to one side; dried fruit breaking away open-ended at the base, the wall subsequently splitting upward into 4 valves; calyx persisting outspread and stiff even after fruit is shed.

GENERAL DISTRIBUTION. Tropical America; introduced and naturalized in parts of the Old World tropics.

DISTRIBUTION IN LESSER ANTILLES. Nevis, Antigua, Montserrat, Guadeloupe, Martinique, St. Lucia, Barbados.

The fruit of this plant gives the appearance of being woody and indehiscent, especially because dehiscence into four valves occurs at the same time as or after the entire fruit wall is cut loose. The indurated style base holds the top of the capsule firmly together, but the walls are thin and brittle. When there is more than one seed developed, one or more in each locule, the fruit appears lobed on the outside.

CULTIVATED SPECIES

The following exotic species are often cultivated.

Argyreia nervosa (Burman f.) Bojer (*A. bracteata* sensu West Indian authors; syn. *A. speciosa* (L. f.) Sweet). COMMON NAMES: liane d'argent, liane à tonnelle, liane de soie, liane à vonvon (Guadeloupe and Martinique); elephant climber (Barbados).

Evolvulus tenuis Martius ex Choisy subsp. *longifolius* (Choisy) Ooststr. (*E. bocasanus* Britton). (Under this name van Ooststroom (1934) cited a specimen from St. Kitts, doubtless the same one recorded by Grisebach as *Evolvulus villosus*). COMMON NAME: lin (Guadeloupe, St. Barts).

Ipomoea batatas (L.) Lam. Locally grown sweet potato (patate douce), an important food item throughout the area.

Ipomoea carnea Jacq. subsp. *fistulosa* (Martius ex Choisy) Austin. COMMON NAMES: ológi di anochi (St. Eustatius, St. Martin); petite campanule (Guadeloupe).

Ipomoea carnea has been reported as cultivated in St. Vincent (Guilding, 1825), and there is the possibility that this was the climbing subsp. *carnea*.

Ipomoea horsfalliae Hooker (*I. pendula* sensu Duss). COMMON NAME: liane rouge à tonnelles (Guadeloupe and Martinique).

In the United States National Herbarium (US), there are three sheets of a specimen (*Fairchild 2768 a, b, c*) collected in St. Lucia in 1932. They bear the following note: " A bona fide *seedling* from the true *Ipomoea horsfalliae Briggsii* vine on Government House, St. Lucia. . . . Mrs. Doorly, wife of the Administrator, planted a few seeds of this vine herself and got a seedling quite distinct from it, which appears to be a . . . reversion to wild type, smaller fl[ower]s and more distinct petals. It appears to be the same as a wild form found along the road to Mr. Knowlton's place, Empire Road, Dominica." As David Fairchild observes, the specimens show a clear resemblance not only to the Jamaican and Puerto Rican species, *I. horsfalliae* Hooker (in Curtis's Bot. Mag. 61: *t. 3315*. 1834), but also to *I. repanda*, which occurs in St. Lucia, Dominica, and throughout the West Indies except Jamaica, and which is, without a doubt, the plant Fairchild saw in Dominica. There seems little question that the garden plant was the hybrid, *I. horsfalliae* × *I. repanda*.

The coloring is like that of both species. It shows progression in leaf-lobing from 3- to weakly 7-lobed. The inflorescence is a dichotomous, very lax corymb; each flower has a slightly curved, cylindrical corolla tube, 3 cm. long and 6–9 mm. wide, with the limb 1 cm. long and lobed for its entire length, the pistil and stamens exserted. The flowers and inflorescence are exactly like those of a robust *Ipomoea repanda*. Flowers of *I. horsfalliae* have corolla tubes slightly longer than those just described, but twice as wide and distinctly narrowing at the base; the limb is only slightly lobed, and the leaves are not just lobed, but definitely palmately compound with 5 leaflets.

Herbarium material often inaccurately labeled *Ipomoea horsfalliae* (cult.) and collected throughout the tropics is mostly of similar hybrid material with lobed leaves and narrow-tubed flowers, scarcely to deeply lobed. Perhaps the cultivated var. *briggsii* is this hybrid.

Porana paniculata Roxb. COMMON NAMES: Chinese lace, white coralita

(St. Eustatius, St. Martin); muguet (Guadeloupe, Martinique); white coralilla (Barbados).

In addition, several native or naturalized species described in the text, including *Merremia tuberosa*, *M. umbellata*, *Operculina ventricosa*, *Ipomoea alba*, *I. cairica*, *I. nil*, *I. quamoclit*, and *I. repanda*, are cultivated.

The following convolvulaceous plants were growing in the botanic gardens of St. Vincent and Martinique in the early nineteenth century. Apart from the species mentioned before in this paper, none of the introduced taxa seems to have survived.

a.) From "Catalogue of Plants in His Majesty's Botanical Garden in the Island of St. Vincent, September 24, 1806" (Guilding, 1825):

COMMERCIAL AND MEDICINAL: *Convolvulus jalapa* [*Ipomoea jalapa*], *C. turpethum* [*Operculina turpethum?*].
ESCULENTS: *Convolvulus batatas* [*Ipomoea batatas*], *C. esculentus* [*Ipomoea batatas*].
MEDICINAL: *Convolvulus brasiliensis* [*Ipomoea pes-caprae* subsp. *brasiliensis*].
EXOTICS, CURIOUS OR ORNAMENTAL: *Convolvulus speciosus* [*Argyreia nervosa*], *C. maximus* [*Ipomoea maxima*], *C. malabaricus* [*Argyreia malabarica?*], *C. maculatus* [?], *C. bicolor* [*Hewittia sublobata*; naturalized in Jamaica], *C. flavus* [*Merremia umbellata* or *M. hederacea*], *C. parviflorus* [*Jacquemontia verticillata*, *J. paniculata*, or *Convolvulus siculus*], *C. quinquefolius* [*Merremia quinquefolia*], *C. pentaphyllus* [*Merremia aegyptia*], *C. dissectus* [*Merremia dissecta*], *C. repens* [*Ipomoea aquatica*, *I. stolonifera*, *Calystegia sepium*], *C. martinicensis* [*Aniseia martinicensis*], *Ipomoea repanda*, *I. carnea*, *I. bona nox* [*I. alba*], *I. filiformis* [*Jacquemontia solanifolia*], *I. coccinea* [*Ipomoea hederifolia?*], *I. speciosa* [*Argyreia speciosa*], *I. umbellata* [*Merremia umbellata*], *I. tuberosa* [*Merremia tuberosa*], *I. macrophylla* [?], *I. grandiflora* [*I. macrantha*], *I. Quamoclit*, flor. coccineis [*I. quamoclit*], *I. Quamoclit*, flor. albis [*I. quamoclit*].

b.) From "Catalogue des Plantes cultivées au jardin botanique et de naturalisation de la Martinique, année 1829" (Delhorme, 1830):

CONVOLVULUS	LISERON	
grandiflorus	grandiflore	[*Ipomoea alba*, *Operculina ventricosa*]
corymbosus	à corymbe	[*Turbina corymbosa*]
batatas	patate	[*Ipomoea batatas*]
dissectus	disséqué	[*Merremia dissecta*]
martinicensus	de la Martinique	[*Aniseia martinicensis*]
IPOMOEA	QUAMOCLIT	
coccinea	écarlate	[*Ipomoea hederifolia?*]
quamoclit	à feuilles ailées	
repanda	ipomée	

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NOMENCLATURAL NOTES ON THE ARACEAE OF THE LESSER ANTILLES

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DURING THE PREPARATION OF a flora of the Lesser Antilles, an attempt has been made to account for all of the scientific names attributed to araceous plants of these islands in the publications of Adams, Boldingh, Britton, Duss, Fournet, Gooding, Grisebach, Hamilton, Hodge, Jacquin, Loveless, Maycock, Plumier, Proctor, Quentin, Stehlé, Swartz, Urban, Vahl, Velez, and Wilson and to report on the typification of the names. The task is not an easy one. Literally no flora is ever complete for all classes of plants. Not all islands of the Lesser Antilles are equally well represented in collections, and the recorded distributions may not be accurate. A few major herbaria may be searched for representative specimens, but to a large extent the compiler of a flora depends on the published literature for records of distribution and hopes that an herbarium specimen will be encountered for verification of locale and identification. Authors may admit the use of sight records or fail to indicate if a specimen was collected. The difficulty and expense of consulting the widely scattered herbaria is obvious, and even in a visit an author may have difficulty finding a specimen. Older herbarium specimens are often without collectors' numbers or may not be specific as to the island of origin. The general designations of "Ind. Occ.," Antilles, Leeward Islands, or West Indies are common in early publications. Locating the modern herbarium in which an old collection may be found presents a special problem, for old collections were bought and sold, divided, or moved many times. Through changes of nomenclature over the years, a specimen may have had several different generic or specific names and may be filed under any one of them.

An investigator of the flora of the West Indies is both fortunate and unfortunate in having to deal with old records. Since the Caribbean Islands were explored early, Linnaean names of widespread species are often based on specimens or descriptions of plants from specific small islands. The original descriptions, however, may be short and inadequate by present standards, and specimens, if preserved, may be fragmentary. Although Linnaeus's *Species Plantarum* is the starting point for the priority of names of recent flowering plants and ferns, only a small percentage of these names have been typified. In the West Indies the typification of species described in the works of Plumier, Jacquin, Swartz, and Duss presents special problems. The original drawings attributed to Plumier are not readily available for consultation, yet comparisons must be made to understand the crude drawings in the published works of Plumier and Burman. Only a few specimens associated with the species Jacquin described are available in Vienna or at the British Museum. Material attributed to Swartz was unnumbered, yet was apparently freely distributed

to several herbaria, and the assembly of such specimens for the proper selection of a lectotype is difficult. During World War II, portions of the herbaria at Berlin and Vienna were destroyed. The classical collections of Araceae were lost, together with more recent collections cited by Engler in his family treatment in *Das Pflanzenreich*. Duss apparently collected several plants under one number and assigned letters as suffixes to these. On other occasions he appears to have gathered plants in different locations and assigned all the same number, while indicating on the labels a variety of locations and dates. Engler and later Urban also subdivided many of the Duss collections, indicating their origin by a suffix letter, with the result that the holotype was kept in Berlin and is no longer extant. Establishing the correct subdivision for duplicates of Duss's collections from other herbaria is a recurring problem, usually not resolved.

There are additional difficulties in studies of the Araceae. The plants are morphologically diverse in development, i.e., juvenile and mature plants may be very different in appearance. Specimens are difficult to collect and to prepare. Some plants are so large, bulky, and fleshy that collectors have avoided making specimens of even average-sized leaves and have instead selected anomalous small plants or gathered only fragments. Many of the species have been described from plants under cultivation in pots or in conservatories. These specimens, too, are atypical as described. Often the area of origin was unknown. Commonly no specimens were preserved, and the living plant no longer exists. Descriptions of sterile, nonflowering plants abound. Characters of horticultural interest often prompted the decision to describe the plant or dominated the descriptions. Competition between fanciers or growers resulted in nearly simultaneous publications, exaggeration of minor differences, and publication in obscure newspapers, seed lists, or journals. For many taxa a neotype should be selected by a monographer. This could be of great value if ample specimens were specially prepared and documented with photographs.

The following notes concern the species attributed to the Lesser Antilles. Many pertain only to the correct bibliographic citation and, in particular, to the notes published serially by Schott in the *Wiener Zeitschrift für Kunst, Litteratur, Theater und Mode* in 1829 and 1830. This is an obscure publication apparently not in American libraries, and I am grateful to Dr. Dan Nicolson for sharing the photographic copy he made in Vienna. In this journal such genera as *Anthurium*, *Dieffenbachia*, and *Monstera* were first validly described and published along with proposed transfers of species; subsequent authors have overlooked these new combinations.

Not all of the problems are solved; many points are only called to the attention of specialists in the family for their future work. I am grateful to Messrs. Thomas Croat, Michael Madison, Simon Mayo, and Dan Nicolson for their consultation, opinions, and sympathetic understanding. Their work will continue on this difficult family.

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Anthurium Schott, Wiener Zeitschr. Kunst 3: 828. 1829.

Schott established the genus *Anthurium*, as indicated, in part of a serial treatment published on August 20, 1829. With this new genus he associated *Anthurium affine*, *Anthurium glaucum* Schott (*Pothos reflexus* Hort. Berol.) and "*crassinervium*, *mycrostachyum*, *myosuroides*, *quinquenervium*, *angustatum*, *pedatum*, *digitatum*, *palmatum*, *gracile*, *lanceolatum*, *acaule*, *violaceum*, *macrophyllum*, *cordatum*" as species of *Pothos* of Swartz, Kunth, and others. On September 8, 1829, he added *Anthurium acaule* (L.) Schott (*Pothos acaulis* L.) and on December 16, 1830, *Anthurium ottonianum* Schott (*Pothos viridis* Hort. Berlin). Since Schott did not generally cite Linnaeus, Jacquin, Willdenow, or earlier authors, the correct basionym must in each case be derived by further search, and the combination must be written invoking the indirect reference permitted by Article 32 (ICBN), especially Note 2.

In 1831, Schlechtendal (Linnaea Litt. Ber. 52) published a commentary supplied by Endlicher on the earlier publication. This has often been regarded as a "reprint," but the text is not an accurate reproduction of the original work. Under *Anthurium*, for example, the same generic diagnosis is supplied, but with the statement "*Pothos* spec. Auct. *americanae*" instead of the list of species indicated above.

A third publication by Schott and Endlicher, *Meletemata Botanica* (1832), attributes many names of taxa to Schott and has been cited frequently by many recent workers as the original place of publication. Under *Anthurium* in this work is the statement: "*A. acaule*, *crassinervium*, *violaceum*, *digitatum*, *undatum*, etc. Schtt. (*Pothi sp. americanae* Auct.)."

Subsequently, the third edition of Sweet's *Hortus Britannicus* (1839), edited by G. Don, contained many combinations of names in the Araceae. This publication has also been cited correctly as the first place of publication in a few cases in the Araceae. However, the entries are abbreviated. Following the specific names are references to authors or books, including "S. M." (Schott's *Meletemata Botanica*, 1832), "R. S." (Roemer & Schultes, *Systema Vegetabilium*, 1818), "H. E. F." (Hooker's *Exotic Flora*, 1823–1827), and "W." (Willdenow, *Species Plantarum*, 1798). In many of these publications the earlier work of Linnaeus and Jacquin is cited, so that by indirect reference the correct bibliographic citation should be (L.) G. Don or (Jacq.) G. Don.

Thus many of the bibliographic citations of *Anthurium* given by Engler in *Das Pflanzenreich* (IV. 23B: 53–295. 1905) are incorrect and must be checked individually. For example, on page 151 Engler published *Anthurium lanceolatum* (L.) Kunth (1841), but on page 293 he corrected this to (Willd.) G. Don in Sweet (1839); it should be (L.) Schott (1829). *Anthurium palmatum* (L.) Kunth (p. 278) is not mentioned in the Addita-

menta but is corrected in the index to (L.) G. Don; it should be (L.) Schott (1829). For *Anthurium acaule* (Jacq.) Schott (p. 69) Engler cited Jacquin's *Selectarum* (1763) but not the *Enumeratio* (1760), and Schott's *Meletemata* (1832) but not the *Wiener Zeitschr. Kunst* reference of 1829 given for the genus. This name is correctly *Anthurium acaule* (Jacq. (1760)) Schott (1829).

Anthurium acaule (Jacq.) Schott, Wiener Zeitschr. Kunst 3: 828. 1829.

Jacquin described *Pothos acaulis* (Enum. Syst. Pl. 31. 1760), citing "Plum. Amer. t. 57 fig. innominata supra fig. i." This plate, correctly numbered 51, is of a woodland scene with many terrestrial and epiphytic aroids illustrated and described in the text. They are subsequently reported to be from various specific islands of the West Indies. A rosette plant above a figure numbered "1" (correctly i) is the plant of reference, and Plumier failed to describe it. Jacquin's description is but one word, "acaulis," which adequately contrasts with the only other species of *Pothos* of that time, *Pothos scandens* L. Three years later in the *Selectarum* (p. 240. *t. 153*. 1763), Jacquin described *Pothos acaulis* in greater detail, supplied an illustration of two detached leaves and an inflorescence, and added an additional reference to Plumier ("amer. . . . t. 62?"), but failed to give a habit sketch comparable to the original Plumier reference or to describe the fruit. The reference that Jacquin questioned is the lectotype of *Pothos lanceolata* L. (Sp. Pl. ed. 2. 1373. 1762). This additional and questionable reference will be discussed later under *Anthurium lanceolatum* (L.) Schott. Engler (Pflanzenr. IV. 23B: 69. 1905) essentially selected a lectotype of *Anthurium acaule* (Jacq.) Schott in the citation of *t. 153* for the basionym and followed that in parentheses with the reference to Plumier's Descr. Pl. Am. ("t. 51, planta innominata supra fig. 1 [i]."

According to Engler, *Anthurium acaule* also occurs in Puerto Rico and the Virgin Islands. Subsequent authors found it in Trinidad and in northern South America as well. Mr. Simon Mayo of Kew has compiled extensive notes on the bird's nest *Anthurium* species and will publish the intricate study he has completed for the Trinidad members of the Araceae. We appear to be in agreement that the name *Anthurium acaule* (Jacq.) Schott is to be applied to the black-gland-dotted, rosette-forming plants of the Lesser Antilles having as synonyms *Anthurium hookeri* Kunth, *Anthurium hookeri* var. *longecuneatum* Engler, and *Anthurium huegelii* Schott (q.v.). Stehlé (Bull. Soc. Bot. France 123: 451. 1976) recognized all three species, and Fournet (Fl. Guadeloupe Martinique, 417–422. 1978) distinguished two of them on a geographical basis and on fruit color. The most common fruit color is chalky to pearly white, with some variation to red or purple reported. On the basis of field observations, extensive collections, and photographs, I conclude that only one species is represented. No collections have been seen from Martinique, however, and further efforts to locate this plant in Martinique are needed.

Anthurium andersonii Schott, Oesterr. Bot. Wochenbl. 7: 325. 1857 = *Anthurium palmatum* (L.) Schott. TYPE: St. Lucia, *Anderson s.n.* Herb. Forsyth (K).

This species is recognized by Jonker and Jonker (Acta Bot. Neerl. 8: 139. 1959) as occurring in "Sta. Lucia, Guadeloupe, Martinique, ?Tobago," and Surinam. The species was not reported by Simmonds in his treatment "The Araceae of Trinidad and Tobago, B.W.I." (Kew Bull. 1950: 391–406. 1951).

Anthurium andraeanum Linden, Illus. Hort. 24: 43. *t. 271.* 1877; *ibid.* 27: 382. 1880. TYPE: cultivated plant originally from Colombia.

Fournet (Fl. Guadeloupe Martinique, 422. 1978) indicates this as "*A.* '*Andreanum*' Hort.," with numerous hybrids and horticultural varieties in cultivation. Others have suggested that the type illustration, of a cultivated plant, represents a hybrid. Plants are grown on St. Lucia and Martinique for the inflorescences, which are sold to tourist boats and exported. Plants naturalized following cultivation have been reported from Dominica.

Anthurium barbadosense Engler, Bot. Jahrb. 25: 404. 1898 = *Anthurium willdenowii* Kunth. TYPE: Barbados, *Eggers 7326.*

Anthurium brachygonatum Schott.

The collection *Duss 523* (NY), with a printed label "Herbier de la Martinique," carries in script an identification and the legend "Hauteur de Mahot, Île de la Dominique." *Anthurium brachygonatum* Schott (Prodr. Syst. Aroid. 468. 1860) was based on a living plant supposedly from Mexico. No material referable to that species is available for comparison. The location on Dominica may be the heights of Mahaut, a town north of Roseau. The specimen consists of two leaves with strong arcuate pinnate venation to the apex and a sterile peduncle from which the bract and spadix are missing. The specimen does not appear to be *Anthurium acaule* in juvenile form and is not recognized.

Anthurium commutatum Schott, Bonplandia 10: 148. 1862 = *A. cordatum* (L.) Schott. TYPE: cultivated plant, origin not stated.

Anthurium concinnum Schott, Oesterr. Bot. Wochenbl. 7: 301. 1857 = *A. cordatum* (L.) Schott. TYPE: St. Vincent, *Guilding s.n.* (K).

Anthurium cordatum (L.) Schott, Wiener Zeitschr. Kunst 3: 828. 1829.

Schott is credited with the transfer of *Pothos cordata* to the genus *Anthurium*, although no use of the basionym by Swartz or Kunth prior to 1829 can be found. Typification is obtained through the work of G. Don

in Sweet (Hortus Brit. ed. 3. 633. 1839), where "R. S." is cited and "Plum. ic. 26. t. 38" is given as a reference to an illustration. Roemer and Schultes (Syst. Veg. 3: 454. 1818) cited a number of references including Willd. Sp. Pl. 1: 685. 1798 (as *Pothos cordata* Willd.) and *t. 38* of both Burman and Plumier. Willdenow cited a Linnaean reference (Sp. Pl. ed. 2. 1373. 1763, *Pothos cordata*) which is also based on Plumier's *t. 38*. By very indirect reference, the correct bibliographic citation is *Anthurium cordatum* (L.) Schott with the basionym *Pothos cordata* L. (Sp. Pl. ed. 2. 1373. 1763) and the lectotype Plumier, Pl. Am. *t. 38*.

Anthurium commutatum Schott, *A. concinnum* Schott, *A. fallax* Schott, *A. guildingii* Schott, and *A. isertianum* Schott are all regarded as synonyms.

Anthurium cordifolium Kunth, Enum. Pl. 3: 76. 1841 = *A. grandifolium* (Jacq.) Kunth.

Kunth cited *Pothos cordata* Willd., excluding the description and synonyms but with reference to the specimen "Herb. 3101." The specimen in the Willdenow Herbarium (IDC 7440. 207: II. 7), as judged from the microfiche reproduction, is a juvenile leaf of *Anthurium grandifolium* taken from a plant in cultivation.

Anthurium costatum Koch & Bouché, Ind. Sem. Hort. Berol. App. 6. 1853; Ann. Sci. Nat. ser. 4. 1: 347. 1854 = *A. grandifolium* (Jacq.) Kunth. TYPE: a cultivated plant, origin unknown.

Anthurium dominicense Schott, Österr. Bot. Zeitschr. 8: 350. 1858. TYPE: Dominica, "Herb. Hooker."

In a later publication Schott (Prodr. Syst. Aroid. 489. 1860) indicated that the type was collected by Imray on Dominica. This species is reported from Dominica, Martinique (Stehlé), and Puerto Rico. Hodge (Lloydia 17: 158. 1954) stated, "Specimens of *A. dominicense* and *A. guildingii* frequently approach one another in vegetative habit. If collections made on other islands, included in the range of these species, show similar intergradations, *A. dominicense* will have to be placed in synonymy under *A. guildingii*." The gradations do occur, but plants from higher elevations in Dominica and from the mountains in Puerto Rico differ from the usual range of leaf shape of *A. cordata* in the prevailing oblong-lanceolate leaf blades which have a grayish cast when dry. For the present, *A. dominicense* is regarded as a distinct species, pending further study in the field.

Anthurium dussii Engler, Bot. Jahrb. 25: 403. 1898 = *A. willdenowii* Kunth. TYPE: Guadeloupe, *Duss 3789*.

This species was not cited by Duss, Stehlé, or Fournet. The holotype, presumably destroyed at Berlin, apparently was not photographed, but an isotype (NY) is clearly referable to *Anthurium willdenowii* Kunth. The

Duss specimen is without data but may represent a plant cultivated in the former St. Pierre Botanical Garden on Martinique.

Anthurium elegans Engler, *ibid.* 1: 482. 1881 = *A. palmatum* (L.) Schott. TYPE: Martinique, *Hahn s.n.*

Engler later placed this *Anthurium elegans* in the synonymy of *A. fissum* C. Koch (Bot. Jahrb. 25: 453. 1898).

Anthurium elegans Engler, Gartenflora 1883: *t. 112.* 1883.

As published, this name is a later homonym and is invalid. The type was a cultivated plant originally collected by Wallis at Buenaventura, Colombia, and the species was renamed *Anthurium fortunatum* Bunting (Baileya 11: 9. 1963). This taxon may be referred to *A. pedatum* (HBK.) Kunth.

Anthurium fallax Schott, Oesterr. Bot. Wochenbl. 7: 309. 1857 = *A. cordatum* (L.) Schott. TYPE: St. Vincent, *Guilding s.n.* (K).

Anthurium fissum C. Koch in Ender, Ind. Aroid. 102. 1864; Regel, Gartenflora 1867: 323. *t. 561.* 1867 = *A. palmatum* (L.) Schott. TYPE: cultivated plant said to be from Colombia, but no recent materials from that country are comparable.

Engler (Pflanzenr. IV. 23B: 278. 1905) referred to this species the collection *Hahn 946* (G-DC, P) from Martinique.

Anthurium gracile (Rudge) Schott, Wiener Zeitschr. Kunst 3: 828. 1829. BASIONYM: *Pothos gracilis* Rudge, Pl. Guianae 1: 23. *t. 32.* 1805.

This species was reported by Duss (Fl. Phan. Antill. Fr. 476. 1897) as once cultivated in the Botanical Garden of St. Pierre, Martinique. The only specimen seen, *Duss 526* (NY), was collected in "1897, 1890" and reported as introduced and cultivated at Fort-de-France, Martinique. Recent collections are known only from the Dominican Republic in the West Indies and from Central and South America.

In recent annotations the combination is attributed to Lindley (Bot. Register 19: *t. 1635.* 1833); Engler had considered it a synonym of *A. scolopendrinum* (Ham.) Kunth. There is a problem here beyond the scope of this study.

Anthurium gracile subsp. **Belangeri** Engler in Bot. Jahrb. 1: 480. 1881.

This name was changed to *Anthurium scolopendrinum* var. *belangeri* (Engler) Engler (Pflanzenr. IV. 23B: 91. 1905) and typified by the collection *Belanger 1067* (P). Although the cited collection has not been seen,

the majority of Belanger's collections have been of cultivated plants from the St. Pierre Botanical Garden, Martinique.

Anthurium grandifolium (Jacq.) Kunth, Enum. Pl. 3: 77. 1841. BASIONYM: *Pothos grandifolia* Jacq. Collect. 4: 121. 1790; Ic. Pl. Rar. 3: *t. 610*. 1792.

Jacquin's plant was from Caracas, Venezuela, but he also cited Plumier (Descr. Pl. Am. *t. 63* and *t. 51, fig. 1* (correctly *i*), which is given without locality). For an understanding of this species and its synonyms, Plumier's *t. 63* should be compared with his *t. 38*, the lectotype of *Anthurium cordatum* (L.) Schott. Synonyms of *A. grandifolium* (Jacq.) Kunth are *Dracontium cordatum* Aublet (not *A. cordatum* (L.) Schott), *Anthurium cordifolium* Kunth, *A. costatum* Koch & Bouché, *A. hahnii* Engler, and *A. wullschlaegelii* Engler.

Anthurium guildingii Schott, Oesterr. Bot. Wochenbl. 7: 301. 1857 = *A. cordatum* (L.) Schott. TYPE: St. Vincent, *Guilding s.n.* (K).

Fournet (Fl. Guadeloupe Martinique, 416. 1978) recognizes *Anthurium guildingii*, as well as *A. isertianum*, from both Guadeloupe and Martinique. The species are distinguished in a key as follows: *A. guildingii* — "Nervures secondaires de la côte 13–14 paires. Pédoncule L ± 35 cm. Spathe large de 10–15 mm., ± décurrente à la base." *A. isertianum* — "Nervures secondaires de la côte 5–7 paires. Pédoncule L ± 20 cm. Spathe large de 15–20 mm., subcordée à la base." These key characters do not agree with those given in the descriptions of the species. They certainly are not observed in specimens from Guadeloupe or Martinique and are not found in Schott's original drawings of the types of the two species.

Anthurium hahnii Engler, Bot. Jahrb. 1: 482. 1885 = *A. grandifolium* (Jacq.) Kunth. TYPE: Martinique, *Hahn 1317* (P).

In a later publication (Pflanzenr. IV. 23B: 190. 1905), Engler cited Hahn "1347." The latter number is probably a misprint, although the Paris specimen has not been located. A specimen of *Hahn 1317* is at Kew.

Anthurium hookeri Kunth, Enum. Pl. 3: 74. 1841 = *A. acaule* (Jacq.) Schott.

This species must be typified by "*Pothos crassinervia* sensu Hooker" (Curtis's Bot. Mag. 57: *t. 2987*. 1830), a plant grown from material said to have been received from Demerara which Hooker thought was *Pothos crassinervia* Jacq. Kunth also referred to a *Pothos acaulis* Hort. Berol., the Hooker illustration, and, with a question mark, to Desfontaines Cat. Pl. 8 and *Pothos solitaria* of Vellozo (Fl. Flum. 9. *t. 123*. 1825).

Anthurium huegelii Schott, Oesterr. Bot. Wochenbl. 5: 83. 1855 = *A. acaule* (Jacq.) Schott.

This name was applied to a cultivated plant called *Anthurium hookeri*, which had auriculate leaf bases. The description mentioned no specimens or illustrations that could be used for typification. In 1860 Schott (Prodr. Syst. Aroid. 469) gave a full description of *A. huegelii* and cited an Imray collection from Dominica, a Guilding collection from St. Vincent, and a Duchassaing collection from Guadeloupe. The synonymy given included *Pothos acaulis* Hooker (Exotic Fl.), *Anthurium neglectum* Miquel, and *Anthurium hookeri* "C. Koch." Engler (Pflanzenr. IV. 23B: 71. 1905) accepted *A. hookeri* Kunth with the exclusion of some unspecified synonyms. He cited *Pothos crassinervia* Hooker (in Curtis's Bot. Mag. **57**: *t. 2987*), *A. huegelii* Schott, and *A. neglectum* Miq. in synonymy. In a footnote he observed that the scarcely auriculate leaf base of *A. hookeri* and the auriculate and obtuse leaf base of *A. huegelii* could be found on the same plant in cultivation. His *fig. 23* of *A. hookeri* shows the auriculate leaf base. Earlier, Engler had described *A. hookeri* var. *longecuneatum* (Bot. Jahrb. **25**: 363. 1898) with leaves to 8 dm. in length and long-cuneate, narrowed at the base, as represented by *H. H. & G. W. Smith 1954* from St. Vincent and *Duchassaing s.n.* from Guadeloupe, both in the Berlin herbarium. Such variation in petiole length and leaf base shape is commonly found in the field in differences between young plants in small rosettes and massive older plants. The species *A. huegelii* and *A. hookeri* and its variety *longecuneatum* are all referred to the synonymy of *A. acaule.*

Anthurium isertianum Schott, Prodr. Syst. Aroid. 493. 1860 = *A. cordatum* (L.) G. Don. TYPE: Guadeloupe, *Isert s.n.* (C).

Anthurium lanceolatum (L.) Schott, Wiener Zeitschr. Kunst **3**: 829. 1829. BASIONYM: *Pothos lanceolata* L. Sp. Pl. ed. 2. 1373. 1762.

Linnaeus cited Plumier, Descr. Pl. Am. 47. *t. 62*. 1693, which is the lectotype. The combination is usually attributed to Kunth (Enum. Pl. **3**: 71. 1841). G. Don (in Sweet, Hortus Brit. ed. 3. 634. 1839) also cited Plumier's *t. 62*, although he did not cite Linnaeus. Schott included "*lanceolatum*" in his list of *Pothos* species to be assigned to his new genus *Anthurium.*

Plumier does not cite a location for the plant illustrated, but Urban (Repert. Sp. Nov. Beih. **5**: 14. 1920) suggested that without doubt the plant was from Martinique, and he also indicated its occurrence in St. Lucia. Collections of Belanger, Hahn, and Duss from Martinique have been assigned to this species, but no reference has been located supporting its occurrence on St. Lucia. The plant that Don cited under the name *Anthurium lanceolatum* was attributed to Barbados and was said to have been introduced into the British Isles in 1790. That reference is probably to a specimen of *A. willdenowii* Kunth.

Fournet (Fl. Guadeloupe Martinique, 417. 1978), in a key to the species, distinguished *Anthurium lanceolatum* from *A. willdenowii* on the basis of spadix length, the former with "spadice L 12–13 cm.," and the latter

with "spadice L 7–9 cm." In discussing *A. lanceolatum*, he wrote, "Ressemble à *A. scandens*. Tige nulle. . . ." Both *A. scandens* and *A. willdenowii* are climbing or scrambling plants, while Plumier's illustration suggests a rosette plant. The drawing does not compare well with any available collections from Martinique. It depicts leaves with connecting veins paralleling the margin and a sharply angled midrib but does not show arcuate secondary veins. The common name "perroquet" is not one applied to aroids in the Lesser Antilles. Engler (Pflanzenr. IV. 23B: 152. 1905) accepted *A. lanceolatum* (L.) Kunth and cited in synonymy *A. martinicense* Engler. He also cited *Belanger 1001* and *Hahn 707* and *1248*, collected in the woods near St. Pierre, and *Duss 2143* and *2144*, from Trois Îlets. The specimens *Belanger 1001* and *Hahn 1248* have not been seen but were the only collections cited in the original publication of *A. martinicense*. A photograph of *Hahn 707*, however, indicates that it, as well as the Duss collections, was found on rocks near Trois Îlets. These do not agree well with Plumier's illustration. For the present it seems advisable to recognize *A. martinicense* and to suggest that *Anthurium lanceolatum* based on *Pothos lanceolata* is an unplaced species.

Anthurium longispathum Carrière, Revue Hort. **60**: 498. 1888 = *A. grandifolium* (Jacq.) Kunth.

This species was based on a plant cultivated in Europe from an introduction from Guadeloupe. The name is a later homonym of *Anthurium longispathum* Schott (Prodr. Syst. Aroid. 520. 1860) which is based on an Oersted specimen from Costa Rica. Engler (Pflanzenr. IV. **23B**: 83. 1905) accepted the Carrière species, although he noted that it was not *A. longispathum* Schott. He was unable to incorporate the species in a key and referred it to a group of "species incerta." Engler suggested it might be the same as *Anthurium grandifolium* (Jacq.) Kunth, an assignment accepted here.

Anthurium macrophyllum (Sw.) Schott, Wiener Zeitschr. Kunst **3**: 828. 1829.

Schott listed "*macrophyllum*" as one of the *Pothos* species of Swartz to be transferred to his new genus, *Anthurium*. *Pothos macrophylla* Sw. (Prodr. 33. 1788), however, is a superfluous name, since he referred to *Dracontium cordatum* Aublet (Hist. Pl. Guiane Fr. 836. 1775) where Plumier's *t. 63*, the lectotype of *A. grandifolium* (Jacq.) Kunth, is cited. Engler (Pflanzenr. IV. **23B**: 83. 1905) was uncertain about the plant Swartz might have had and suggested that *A. macrophyllum* be deleted.

Anthurium macrophyllum G. Don in Sweet, Hortus Brit. ed. 3. 633. 1839 = *A. grandifolium* (Jacq.) Kunth.

Don cited "R. S." as the implied source of the specific epithet and Jacquin, Ic. 3. *t. 610* as a reference to an illustration. Roemer and Schultes (Syst. Veg. **3**: 455. 1818) referred to Swartz, Willdenow, and Jacquin.

Anthurium macrophyllum Endlicher ex Grisebach, Fl. Brit. W. Indian Is. 508. 1864 = *A. grandifolium* (Jacq.) Kunth.

This name cannot be traced to any publication by Endlicher. Grisebach made reference to Plumier's *t. 63*, Jacquin's *t. 610*, *Pothos* Sw., and *P. grandifolia* Jacquin.

Anthurium martinicense Engler, Bot. Jahrb. 1: 480. 1881. TYPE: *Belanger 1001* and *Hahn 124* (P) were cited in the original description.

Although Engler (Pflanzenr. IV. 23B: 151. 1905) reduced this species to the synonymy of *A. lanceolatum* (L.) Kunth, that action does not seem justified.

Anthurium neglectum Miquel, Catal. Horti Bot. Amstelod. 1853.

This name was cited in synonymy by Engler (Pflanzenr. IV. 23B: 71. 1905) when he accepted *A. hookeri* Kunth. As listed on the unnumbered third page of the 1853 *Catalogue*, the name is without description. In the 1857 issue of the *Catalogue*, Miquel and Groenewegen list "*A. neglectum* Hort." in the synonymy of *A. hookeri*, correctly *A. acaule* (Jacq.) Schott, again without description.

Anthurium scandens (Aublet) Engler in Martius, Fl. Brasil. 3(2): 78. 1878. BASIONYM: *Dracontium scandens* Aublet, Pl. Guian. 2: 836. 1775. LECTOTYPE: Plumier, Descr. Pl. Am. *t. 78*.

Aublet cited *t. 74* instead of *t. 78* in Plum. Descr. Pl. Am. and gave the type location as Port de Paix in Haiti. I have seen no specimens of this taxon from the Lesser Antilles. Grisebach (Fl. Brit. W. Indian Is. 508. 1864) cited a Wullschlaegel specimen from Antigua, but notes by Box in the British Museum indicate that he could not find it during his long period of collecting on that island. Duss (Fl. Phan. Antill. Fr. 474. 1897), without citing specimens, reported the plant to be "peu abundant" on Guadeloupe but absent from Martinique. Stehlé (Bull. Soc. Bot. France 123: 450. 1976) listed *Anthurium scandens* var. *violaceum* in a key but did not specify the island. Fournet (Fl. Guadeloupe Martinique, 419. 1978) reported the species from Deshaies and Vieux-Habitants on Guadeloupe and said that, according to Velez, plants from Martinique were recorded by Stehlé.

It is recognized today that the fruits of *Anthurium scandens* can be white or purplish. The existing nomenclature for subspecific taxa is confused, since it is largely based on *Pothos violacea* Sw. (Prodr. 32. 1788), which is an illegitimate renaming of *Dracontium scandens* Aublet. Schott (Wiener Zeitschr. Kunst 3: 828. 1829) listed "*violaceum*" among *Pothos* species of Swartz to be transferred to *Anthurium*. In 1841 Kunth (Enum. Pl. 3: 68) described *A. violaceum* forma *angustifolia* Kunth, the type being a white-fruited cultivated plant in Berlin. In 1864 Grisebach (Fl.

Brit. W. Indian Is. 507) recognized from Haiti variety *angustifolia* Kunth with white berries. Engler (Martius, Fl. Brasil. 3(2): 78. 1878) recognized *A. scandens* var. *violaceum* (Sw.) Engler, thereby including the lectotype of the species; var. *leucocarpum* (Schott) Engler (basionym: *A. leucocarpum* Schott, Prodr. Syst. Aroid. 437. 1860); and, as a synonym, *A. violaceum* forma *angustifolia* Kunth.

Anthurium swartzianum Schott, Oesterr. Bot. Wochenbl. 7: 238. 1857. TYPE: Ind. Occ. (s).

The unlocalized specimen in the herbarium at Stockholm is *Anthurium willdenowii* Kunth, which is common today in Barbados.

Anthurium violaceum (Sw.) Schott, Wiener Zeitschr. Kunst 3: 828. 1829 = *A. scandens* (Aublet) Engler. BASIONYM: *Pothos violacea* Sw. Prodr. 32. 1788.

Swartz cited Browne (Hist. Jam. 333. 1756) and Aublet (Hist. Pl. Guiane Fr. 836. 1775) (*Dracontium scandens*). The name was superfluous when published.

Anthurium willdenowii Kunth, Enum. Pl. 3: 71. 1841. TYPE: "*Pothos lanceolata* Willd., *Herb. Willd. 3095*," not L.

The plant described was cultivated in Berlin; its country of origin was unknown. Schott (Prodr. Syst. Aroid. 479. 1860) attributed the species to St. Lucia on the basis of a Herb. Forsyth specimen in Herb. Bentham, and he saw cultivated material as well. A specimen at Kew bears a printed label, "St. Lucia, Anderson." Anderson, the director of the botanic garden on St. Vincent, acquired material from various areas in the Caribbean, some of which was transshipped to England. Engler (Bot. Jahrb. 25: 480. 1898) assigned this name to collections from Brazil and later (Pflanzenr. IV. 23B: 150. 1905) cited only material from that country. Simmonds (Kew Bull. 1950: 395. 1951) considered "*Anthurium willdenovii* Kunth sensu Schott" to be from Tobago and St. Lucia, the latter on the basis of the Anderson specimen. He noted that the Brazilian specimens Engler cited from the Kew herbarium (*Glaziou 9026, 17335*) "do not match the Broadway collection. Probably two species are involved." Gooding *et al.* (Fl. Barbados, 89. 1965) accepted *A. willdenowii*, cited in synonymy *A. barbadosense*, and stated the range to be Barbados, Tobago, and Brazil. Unfortunately no material cited by Engler has been available for study. If it should prove to be distinct, then an alternate or new name is required for the South American plants.

As synonyms of *Anthurium willdenowii* I recognize *A. barbadosense*, *A. dussii*, and *A. swartzianum*.

Anthurium wullschlaegelii Engler, Bot. Jahrb. 25: 434. 1898 = *A. grandifolium* (Jacq.) Kunth. TYPE: Antigua, *Wullschlaegel 551* (GOET).

Caladium Ventenat, Descr. Cels, *pl. 30*. 1801.

The usual bibliographic citation for this genus is Ventenat in Roemer, Arch. Bot. 2(2): 347. 1800, but Ventenat also gave a complete generic description in the text accompanying *plate 30* in *Descriptions des Plantes . . . cultivées dans le Jardin de J. M. Cels*. According to Stafleu (Reg. Veg. **52**: 397, 482. 1976), *plate 30* of Descr. Cels was published 1 March 1801, and page 347 of Roemer, March–December 1801. However, in the Roemer reference Ventenat cited Descr. Cels, *pl. 30*, suggesting the correct priority of the two descriptions.

Caladium bicolor forma **rubicundum** (Engler) Stehlé, Bull. Soc. Bot. France **123**: 452. 1976 = *C. bicolor* (Aiton) Vent.

Caladium bicolor forma **surinamense** (Miq.) Stehlé, *ibid.* = *C. bicolor* (Aiton) Vent.

The combinations published by Stehlé are illegitimate, since they were published without citation of the basionyms. Engler (Martius, Fl. Brasil. 3(2): 181. 1878) had listed "Rubicundeum Engl." as an undesignated subspecific taxon but later (Pflanzenr. IV. **23E**: 32. 1920) treated this as variety *rubicundum* Engler. Also in 1878, Engler listed *Caladium surinamense* Miq. as an unnamed form under the taxon "Regale." Since only leaf color is involved, the Lesser Antillean plants would be better considered among the myriad of selected cultivars.

Colocasia Ray ex Schott in Schott & Endlicher, Melet. Bot. 18. 1832.

The generic name *Colocasia* Schott in Schott & Endlicher is conserved over *Colocasia* Link (1795). Schott attributed the name to Ray, although no reference is given.

The conserved type species is *Colocasia antiquorum* Schott, a renaming of *Arum colocasia* L. (Sp. Pl. 965. 1753), a Mediterranean species. The oldest specific epithet, however, is *Colocasia esculenta* (L.) Schott (basionym: *Arum esculentum* L.), considered to be a neotropical species. Some authors apply *C. antiquorum* to wild plants and *C. esculentum* to cultivated plants, while others have regarded one as a synonym of the other. To the best of my knowledge, a lectotype has not been chosen for either species. Linnaeus cited several references in his publication of *Arum colocasia*. These should be considered and compared with the specimen in the Linnaean Herbarium (*1079.4*). A second specimen in that herbarium (*1079.5*), *Arum esculentum*, should be considered in relation to the illustration of Sloane (Voy. Is. Nat. Hist. *t. 106, fig. 1*) or supporting herbarium material of it. Both "species" of *Colocasia* are presumably natives of tropical Asia.

Dieffenbachia Schott, Wiener Zeitschr. Kunst 3: 802. 1829.

The generic name is usually attributed to Schott in Schott and Endlicher, Melet. Bot. 20. 1832, but was actually published earlier. The transfer of *Caladium seguinum* Ventenat was proposed as *D. seguinum* Schott. *Caladium seguinum* Ventenat (Descr. Cels, text for *pl. 30*. 1801) was the implied transfer of *Arum seguine* L. (Sp. Pl. ed. 2. 1371. 1763) to the newly created genus *Caladium* Vent. The correct basionym is *Arum seguine* Jacq. (Enum. Syst. Pl. 31. 1760), now known as *Dieffenbachia seguine* (Jacq.) Schott. Although Jacquin cited only Plumier, Descr. Pl. Am. *t. 51h*, *plate 61* and a description by Plumier on page 45 are also associated with this species.

Dieffenbachia maculatum (Loddiges) G. Don in Sweet, Hortus Brit. ed. 3. 632. 1832. BASIONYM: *Caladium maculatum* Loddiges, Bot. Cab. 608. 1822 = *D. seguine* (Jacq.) Schott.

Bunting (Baileya **10**: 145. 1962) proposed the combination *D. maculata* (Lodd.) Bunting and later corrected the error (Baileya **11**: 3. 1963). Some herbarium material is still annotated as *Dieffenbachia maculata*.

Dieffenbachia plumieri Schott, Oesterr. Bot. Wochenbl. 2: 69. 1852 = *D. seguine* (Jacq.) Schott. TYPE: "icone Plumieri Mart."

Monstera Adanson, Fam. Pl. 2: 470. 1763.

Reference: Madison, M. A revision of *Monstera* (Araceae). Contr. Gray Herb. **207**: 3–100. 1977.

Monstera adansonii Schott, Wiener Zeitschr. Kunst 4: 1028. 1830.

This common species is usually called *Monstera pertusa* (L.) deVriese (Hortus Spaarn-Berg. 1839) with the basionym *Dracontium pertusum* L. (Sp. Pl. 967. 1753). The name and combination are illegitimate because of *Monstera pertusa* (Roxb.) Schott (Wiener Zeitschr. Kunst **4**: 1028. 1830) with a basionym *Pothos pertusa* Roxb. (Fl. Indica **1**: 455. 1820). Schott renamed *Dracontium pertusum* Miller (Gard. Dict. ed. 8. 1. 1768) as *Monstera adansonii* Schott. Miller had cited both Linnaeus (Sp. Pl. 968) and Plumier (*t. 56*). The Plumier plate has been designated the lectotype.

The following are synonyms:

Monstera jacquinii Schott, Oesterr. Bot. Wochenbl. **4**: 66. 1854. TYPE: Jacquin, Pl. Rar. Horti Caes. Schoenbr. **2**: *tt. 184*, *185*. 1797.

Monstera imrayana Schott, Österr. Bot. Zeitschr. **9**: 40. 1859. TYPE: Dominica, *Imray 333* (K).

Monstera macrophylla Schott, Prodr. Syst. Aroid. 362. 1860. TYPE: Guadeloupe, *Perrotet s.n.* (W — destroyed).

Montrichardia Crueger, Bot. Zeit. 12: 25. 1854.

This name has been conserved over *Pleurospora* Rafinesque (1838), with the type species indicated as *M. aculeata* (G. F. W. Meyer) Schott. The correct bibliographic citation is unclear. In describing the genus, Crueger mentioned *Caladium aculeatum* Meyer, but the combination was implied and not stated. In 1856 Schott (Synopsis Aroid. 1: 72) attributed the name to himself with the initial "S." Grisebach (Fl. Brit. W. Indian Is. 510. 1864) did not use a parenthetical author but attributed the name to Crueger without a reference. He also cited *Montrichardia arborescens* (L.) Schott and *M. aculeata* Crueger, giving in the synonymy of the latter species *Caladium* Meyer and *C. arborescens* Meyer.

Material from the Lesser Antilles has been variously identified as *Montrichardia arborescens* (L.) Schott, *M. aculeata* (Meyer) Schott, and *M. linifera* (Aublet) Schott. The differences described in the leaf base, the size of the plants, and the spininess of the stems can all be found in one population. The plants produce a terminal inflorescence with subsequent lateral or sympodial growth of one or several shoots. The first leaves produced on the sympodial growth, which are apt to be collected with the inflorescence, have a tendency toward a sagittate base. Leaves collected from the smaller, nonflowering stems often have a cordate base with the lobes overlapping. The spines may be developed either only in the lower internodes or throughout the plant, even on the flowering shoots. There appears to be but one species in the genus.

Montrichardia arborescens (L.) Schott. BASIONYM: *Arum arborescens* L. Sp. Pl. 967. 1753. LECTOTYPE: Plum. Descr. Pl. Am. *tt. 51g, 60.*

Philodendron Schott, Wiener Zeitschr. Kunst 3: 780. 1829.

This name is a conserved spelling over the original *Philodendrum*. The type species is indicated as *Philodendron grandifolium* (Jacq.) Schott, obtained by indirect reference. Schott cited as the basionym "*Caladium grandifolium* W.," while Willdenow (Sp. Pl. 4: 490. 1798) cited Jacquin. The lectotype is Jacquin, Pl. Rar. Horti Caes. Schoenbr. *2*: 34. *t. 189.* 1797.

Philodendron dispar Schott, Synopsis Aroid. 79. 1856 = *P. lingulatum* (L.) C. Koch.

The illustration by Plumier, Descr. Pl. Am. *t. 37*, is the lectotype of both *Philodendron dispar* Schott and *Arum lingulatum* L. (*Philodendron lingulatum* (L.) Koch, 1855).

Philodendron dussii Engler, Bot. Jahrb. 26: 530. 1859.

The original publication cited only the collection *Duss 2153*, made in Guadeloupe. Dr. Michael Madison informed me that such a collection still exists in Berlin and appears to be the basis for the illustration in *Das Pflanzenreich* (IV. 23Db: 63, *fig. 22*. 1913). The sheet bears two labels. The original, "Père Duss — Plantes de la Martinique," has the identification *Philodendron hederaceum* Schott and the data, "Grimpant. Bois du Parnasse. Ajoupa Bouillon." A second label, printed "Herbarium Krug & Urban," has the number *2153* crossed out and *2149* with an undecipherable suffix letter written in. The location is given as Martinique, and the determination *Philodendron dussii* Engler is noted as "det Engler 1890."

The species was not mentioned by Stehlé or Fournet and has not been re-collected. A Duss collection numbered *4526* (US), without data other than the general locality of Martinique, was identified as *Philodendron dussii* Engler but was correctly annotated by Bunting as *Philodendron scandens* Koch & Sello subsp. *isertianum* (Schott) Bunting.

The renumbering of this collection to *2149* clearly points out the difficulty of working with Duss collections. In his *Flore phanérogamique des Antilles françaises*, the following collections are cited: *2149*, *Xanthosoma hastifolium*, p. 481; *2149b*, *Dieffenbachia seguine*, p. 477; *2149b*, *Philodendron dispar*, p. 479; *2149c*, *Philodendron hederaceum*, p. 479; *2149c*, *Acontias helleborifolius*, p. 481; *2149d*, *Xanthosoma sagittifolium*, p. 481.

Philodendron giganteum Schott, Synopsis Aroid. 89. 1856. TYPE: cultivated plant, origin uncertain.

Philodendron isertianum Schott, Prodr. Syst. Aroid. 242. 1860. TYPE: Martinique, *Isert s.n.* (C).

This is treated by Bunting (Gentes Herb. 10: 163. 1968) as *Philodendron scandens* subsp. *isertianum* (Schott) Bunting.

Philodendron lingulatum (L.) C. Koch, Ind. Sem. Hort. Berol. App. 2. 1855.

For the basionym of *Arum lingulatum*, Linnaeus (Sp. Pl. ed. 2. 1371. 1763) cited references to Browne, Sloane (Voy. Is. Nat. Hist. 78. *t. 27, fig. 2*), and Plumier "Spec. 4, ic. 37" (Cat. 4, Pl. Am. Burm. *t. 37*. 1755). The most accurate representation is the Burman plate, which might be designated the lectotype after comparative study with the specimen in the Linnaean Herbarium (*1079.17*).

Philodendron scandens C. Koch & H. Sello, Ind. Sem. Hort. Berol. App. 4. 1853.

The original publication has not been seen, but Bunting's treatment (Gentes Herb. 10: 136–168. 1968) is accepted for the species. There is some difficulty recognizing his subspecies in the field except by geographical location.

Philodendron swartzianum Schott, Oesterr. Bot. Wochenbl. 7: 237. 1857 = *P. lingulatum* (L.) C. Koch. TYPE: St. Kitts, *Euphrasen s.n.* (S).

Pistia L. Sp. Pl. 963. 1753.

Pistia stratiotes L. Sp. Pl. 963. 1753.

Linnaeus cited references applying to plants of Asia, Africa, and the Americas. The typification of the species is uncertain. Presl (Epimeliae Botanicae, 240. 1849) redefined *Pistia stratiotes*, limiting the species to the Luzon province of the Philippines and citing "Cuming pl. phil. n. 1114." Additional species from South America and Africa were described. I am hesitant to consider Presl's action a neotypification of this widespread species.

Xanthosoma Schott in Schott & Endlicher, Melet. Bot. 19. 1832.

Xanthosoma requires a critical revision. Few names in use in the Lesser Antilles are valid and in accordance with the rules of nomenclature.

Xanthosoma atrovirens C. Koch & Bouché, Ind. Sem. Hort. Berol. App. 3. 1854.

Duss (Fl. Phan. Antill. Fr. 481. 1897) and Fournet (Fl. Guadeloupe Martinique, 428. 1978) have reported this species from several locations on Martinique and Guadeloupe. The typification of the species and the correct application of the name are questionable. Koch and Bouché cited Sloane (Voy. Is. Nat. Hist. *t. 106, fig. 2*) and reported that cultivated material they had seen was obtained by Moritz in Venezuela. The Sloane illustration, however, is the lectotype of *Xanthosoma sagittifolium* (L.) Schott, and the plant described requires reevaluation by a monographer.

Xanthosoma caracu Koch & Bouché. *ibid.*

This name is often attributed incorrectly to Koch and Sello. Stehlé (Bull. Soc. Bot. France 123: 452. 1976) reported the species from the French islands. This was noted but uncorroborated by Fournet (Fl. Guadeloupe Martinique, 428. 1978).

The original description is of sterile juvenile cultivated material of unknown origin. It is doubtful if this name can ever be applied correctly, since no authentic material is known.

Xanthosoma jacquinii Schott in Schott & Endlicher, Melet. Bot. 19. 1832 = *Xanthosoma undipes* (Koch) Koch, Bonplandia 4: 3. 1856.

Nicolson (Taxon 24: 346, 347. 1975) has discussed the correct name for *Xanthosoma jacquinii* Schott, noting that Schott applied the epithet to two different plants.

Xanthosoma ? peregrinum (L.) Grisebach, Fl. Brit. W. Indian Is. 511. 1864.

Grisebach apparently used the question mark to indicate an uncertainty for the transfer of *Arum peregrinum* L. to *Xanthosoma*. He cited material from Jamaica and a distribution in Guadeloupe and Venezuela. The name is not currently used in floras of Jamaica or the Lesser Antilles.

Schott (Prodr. Syst. Aroid. 596. 1860) suggested, also with a question, that *Arum peregrinum* L. might be the same as *Alocasia macrorrhiza* (L.) Schott, and this treatment is followed by Engler (Pflanzenr. IV. 23E: 84. 1920). Engler (*ibid.*, p. 50) also cited "?*X. peregrinum* Griseb." as a possible synonym of *Xanthosoma atrovirens* Koch & Bouché.

Xanthosoma roseum Schott, Österr. Bot. Zeitschr. **8**: 178. 1858; Prodr. Syst. Aroid. 180. 1860.

This species may be typified by *Hoffman s.n.* from Costa Rica. Engler (in Martius, Fl. Brasil. 3(2): 189. 1879) reported this species from Guadeloupe on the basis of a collection by Duchassaing, which has not been seen. No recent work on the Antilles considers this species. Standley and Steyermark in the *Flora of Guatemala* (Fieldiana Bot. 24(1): 360. 1958) list the species as a synonym of *Xanthosoma robustum* Schott, limited in distribution to Central America.

Xanthosoma sagittifolium (L.) Schott in Schott & Endlicher, Melet. Bot. 19. 1832.

Nicolson (Taxon 24: 345–347. 1975) proposed that this species be selected as the lectotype of the genus. He failed to consider the problem of selecting a lectotype for the basionym *Arum sagittaefolium* L. In the original description Linnaeus (Sp. Pl. 966. 1753) cited Hortus Cliff. "345," Royen ("lugdb. 8"), Sloane ("jam. 63, hist. 1, p. 167 t. 106. f. 2 [leaf only]"), and Plukenet ("phyt. 149 f. 2" — a crude sketch of a large cormose base, inflorescence, and leaves). The correct citation for *Hortus Cliffortianus* is page 435, where Linnaeus stated that the Sloane plate was good but the Plukenet illustration was not. Clearly Linnaeus was accepting the Sloane illustration, even though it is but a leaf, as representative of his species.

In discussion of "*Xanthosoma belophyllum* (Kunth) C. Koch," Koch (Ind. Sem. Hort. Berol. App. 3. 1854) concluded that four species were represented under "*Ari sagittifolii* Linnaeus." The Sloane reference, he stated, was *Xanthosoma atrovirens* C. Koch & Bouché, a new species. Koch did recognize "*X. sagittifolium* (Schott) C. Koch" and cited as a synonym "*Arum sagittifolium* L. ex p., Jacq. hort. Vind. II 157."

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NOMENCLATURAL NOTES ON SOME LESSER ANTILLEAN MONOCOTYLEDONEAE

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THE FOLLOWING NOTES were assembled from a study of literature and herbarium references to the occurrence of various Monocotyledoneae in the Lesser Antilles.

AMARYLLIDACEAE

Herbarium specimens of *Crinum* from the Lesser Antilles are few in number, fragmentary, and poorly preserved. They represent plants introduced, once cultivated, and now persisting in cemeteries and near present or former churches or settlements. They have proven to be hardy, often forming extensive mats or "fairy rings" as the colony spreads outwardly while dying in the middle.

Uphof (Herbertia 9: 63. 1942) chose *Crinum latifolium* L., the first species of *Crinum* mentioned by Linnaeus, as the type species. However, Britton and Wilson (Sci. Survey Porto Rico Virgin Is. 5: 160. 1924) had previously designated *C. americanum* L. as the type species, and this is accepted in the *Index Nominum Genericorum*.

The nomenclature of the species of *Crinum* is complex. The work of Milne-Redhead and Schweickerdt (Jour. Linn. Soc. Bot. 52: 160–162. 1939) in establishing the name *Crinum bulbispermum* (Burman) Milne-R. & Schweick. clearly shows the problems of tracing names through an extensive and complicated horticultural literature. The publication "Garden Crinums" by L. S. Hannibal (Bull. Louisiana Soc. Hort. Res. 3: 219–322. 1972) has been useful. Mr. Hannibal kindly commented on questions presented to him and annotated specimens. His opinions are accepted here.

Crinum amabile Ker-Gawler

This name, usually attributed to Donn (Hortus Cantabrig. ed. 6. 83. 1811; reported as "fine"), is a *nomen nudum*. Ker-Gawler first described the plant in Curtis's Bot. Mag. 39: *t. 1605*. 1814. That illustration, prepared from a cultivated plant introduced by Roxburgh from the East Indies, is designated as the lectotype. Later, Ker-Gawler (Jour. Sci. Arts 3: 111. 1817) published a second description with the notation "Nobis."

Crinum americanum sensu Duss, Fl. Phan. Antill. Fr. 560. 1897.

When distributed, herbarium specimens collected by Duss were given several numbers and locations. I have seen two sheets of *Duss 3716* —

one is *Crinum asiaticum* L.; the other, *Crinum loddigesianum* Herb. A second collection, *Duss 3491*, consists of two sheets: one, labeled *Crinum americanum*, is a hybrid *Hippeastrum* of the *H. reginae* complex; the other, labeled *Hymenocallis americana*, is a form of *Crinum americanum*. All are from cultivated plants.

Crinum asiaticum L. Sp. Pl. 292. 1753.

In the original description, Linnaeus cited Fl. Zeyl. no. 127 (p. 53), Hermann, Horti Acad. Lugdb.-Bat. 682, 683, and Rheede, Hortus Ind. Malab. 11: 75. *t. 38*. Ker-Gawler (Jour. Sci. Arts 3: 105, 110. 1817) cited the Rheede reference when he described *Crinum defixum*, a sessile-flowered species. He recognized *Crinum asiaticum* L., a pedicellate-flowered plant, cited the Hermann reference, and suggested as a modern plate Curtis's Bot. Mag. 27: *t. 1073*. 1807. Hannibal (Bull. Louisiana Soc. Hort. Res. 3: 309, 313. 1972) accepted both *C. asiaticum* and *C. defixum* but under the former noted the Rheede reference and commented, "Evidence indicates this plant was the original *C. asiaticum* Linn."

Crinum erubescens L. f. ex Aiton, Hort. Kew. 1: 413. 1789.

Aiton attributed this name to Linnaeus filius, although its use by him has not been located. Ker-Gawler (Curtis's Bot. Mag. 30: sub. *t. 1232*. 1809) suggested the reference was to a manuscript name. Aiton also cited Miller, Fig. Pl. Gard. Dict. 73. *t. 110*. 1760, which might be regarded as a possible lectotype. However, Miller stated of the flowers, "These are of a beautiful white colour," which does not agree with the red or rose color associated with the species in modern floras. Ker-Gawler later referred the Miller plate to *Crinum asiaticum* (Curtis's Bot. Mag. sub *t. 1073*. 1807), although the plant Miller illustrated has wider perianth segments than those generally associated with that species. It is appropriate to consider Curtis's Bot. Mag. *t. 1073* the lectotype of *Crinum asiaticum*.

"**Crinum caribaeum** Bauer," *Crinum caribaeum* Baker = *Crinum floridanum* Fraser ex Griseb.

Fournet (Fl. Guadeloupe Martinique, 237. 1978) used the name "*Crinum caribaeum* Bauer" for a plant introduced in certain gardens in Guadeloupe and Martinique. The Bauer reference cannot be traced, but since Fournet cited as a synonym "*Crinum floridanum* Griseb., non Fraser," it is apparent the authority intended was Baker. Baker (Gard. Chron. n.s. 16: 40. 1881) had published *Crinum caribaeum* Baker (*C. floridanum* Griseb. Fl. Brit. W. Indian Is. 583, non Fraser) and wrote, "Gathered in Jamaica by the Rev. Wullschlaegel, *C. floridanum* of Fraser as already stated proved to be *C. asiaticum*. The alliance of this is with *C. bracteatum*." In a discussion of *Crinum asiaticum* printed in an earlier part of the series (Gard. Chron. n.s. 15: 786. 1881), Baker had written, "*C. floridanum* of Fraser is the plant mentioned by Herbert in his Amaryllidaceae as identical with

typical *asiaticum*, of which 'a great bulb surrounded by offsets was brought from Florida by Fraser, who assured me he had dug it up on the seaside.' Kunth misprints this name *floridum*, and Grisebach uses the name for a Jamaican plant which is evidently quite distinct." Herbert (Amaryllidaceae, 243. 1837), under *Crinum asiaticum* var. *toxicarium*, had stated, "A great bulb of this plant surrounded by offsets was brought from Florida by Fraser, who assured me that he had dug it up on the seaside. It must have been washed ashore from some ship that was bringing it from the east." Fraser's *Catalogue* of 1813, as reprinted by Greene (Pittonia 2: 114–119. 1890), does not list any plant recognizable as a *Crinum* or an *Amaryllis*. In fact, Grisebach (Fl. Brit. W. Indian Is. 583. 1864) wrote, "*Crinum floridanum*, Fraser (inedit.)" and "I adopt Fraser's name on account of the resemblance of this species with *C. bracteatum* W. (Jacq. Schoenbr. 4. t. 495; *C. asiaticum*, Red. Lil. 6. t. 348), to which Fraser's plant was reduced by Ker. The lesser number of flowers, the narrow petiole, the bulb probably less columnar, and the American habitat speak for its peculiarity: if however, it should not prove distinct, Willdenow's name is to be adopted, as *C. asiaticum*, L., rests chiefly upon the authority of Rumphius. . . ." For the habitat Grisebach cited "Jamaica!, Wullschl.; [an island near the coast of Florida, along the sea (Fras.)]." The earlier publication of *Crinum floridanum* Fraser by Herbert (Curtis's Bot. Mag. sub. *t. 2121*. 1820) lacks descriptive information and should be considered a *nomen nudum*. In *Index Kewensis* this name is misspelled as "*C. floridum*" and reported to be the same as *C. asiaticum*. The Wullschlaegel collection has not been seen but must be considered the type of *Crinum caribaeum*. Adams (Fl. Pl. Jamaica, 1972) does not mention *C. caribaeum* or *C. asiaticum*; however, Hannibal (Bull. Louisiana Soc. Hort. Res. 3: 246. 1972) refers to "this small Jamaica plant" and notes that it is semitender. Unfortunately, on page 307 Hannibal refers to his *fig. 16* as *Crinum caribaeum*, but the legend on page 245 is *C. oliganthum*.

Crinum floridanum Fraser ex Griseb. is published with a description and the citation of a specimen and should be accepted. *Crinum caribaeum* Baker, based on the same type, is a later synonym.

Crinum giganteum sensu Duss, Fl. Phan. Antill. Fr. 560. 1897.

The collection cited, *Duss 2142*, as represented by a specimen in the herbarium of the New York Botanical Garden, is a species of *Hippeastrum*. That specimen was collected in 1886 in the St. Pierre Botanical Garden, Martinique, from an introduced and cultivated plant. Fournet (Fl. Guadeloupe Martinique, 237. 1978) suggested that plants today cultivated as *C. giganteum* are allied to *C. americanum*.

Crinum longiflorum sensu Duss, Fl. Phan. Antill. Fr. 560. 1897.

One specimen (*Duss 3833* (NY)) labeled *Crinum longiflorum* is *C. bulbispermum*; several localities are given on the label. Other collections so

named (*Duss 2134, 3491* (both NY)) have been identified by L. S. Hannibal as *Crinum americanum* subsp. *robustum* Hannibal.

Crinum zeylanicum (L.) L.

This taxon needs typification. Hannibal (Bull. Louisiana Soc. Hort. Res. 3: 268. 1972) accepted the species and noted, "This is the dustbin of the *Crinum* as it contains a wide variety of forms ranging from southern Asia to tropical east Africa." *Amaryllis zeylanicum* L. (Sp. Pl. 293. 1753) was transferred to *Crinum* by Linnaeus (Syst. Nat. ed. 12. 2: 236. 1770). Hooker (in Trimen, Handb. Fl. Ceylon 4: 272. 1898) considered it a variety of *Crinum latifolium*, and this is accepted in *Hortus III* (p. 334. 1976).

Eurycles amboinensis (L.) Lindley in Loudon, Encycl. 242. 1841.

The basionym is *Pancratium amboinense* L. (Sp. Pl. ed. 2. 1: 419. 1762); *Eurycles sylvestris* Salisbury (Trans. Hort. Soc. London 1: 337. 1882. Type: *Herb. Banks*) is considered a synonym. This species is reported to be in cultivation on St. Martin, St. Eustatius, and Saba by Fr. Arnoldo (Gekw. Nutt. Pl. Nederl. Antill. 70. 1971), and on the French islands by Fournet (Fl. Guadeloupe Martinique, 239. 1978) under the synonymous name. It is called "Brisbane lily" in the Dutch islands and "lis de Madagascar" on the French islands. Its origin is stated to be Amboina.

Haemanthus multiflorus Martyn [Monog. cum Ic.; et] ex Willd. Sp. Pl. 2: 25. 1799.

This species is under cultivation in the Lesser Antilles but is poorly represented in herbaria. Fournet's statement (Fl. Guadeloupe Martinique, 239. 1978) that the taxon is often placed in the separate family Haemodoraceae is in error.

Hippeastrum puniceum (Lam.) Kuntze, Rev. Gen. Pl. 2: 703. 1891.

In many recent publications this combination is credited to Voss in Vilmorin, Blumengartnerei, ed. 3. 1033. 1895. In making the transfer, Kuntze misspelled as "purpureum" the specific epithet of *Amaryllis punicea* Lam.; Voss corrected this error.

Hippeastrum puniceum (Lam.) Urban var. **mariae-galante** Stehlé, Bull. Soc. Bot. France 123: 446. 1976.

This varietal name is used in a key to the Monocotyledoneae of the French islands without Latin description or citation of specimens and so is illegitimate.

Hymenocallis Salisbury, Trans. Hort. Soc. London 1: 338. 1812.

Salisbury's original description of this genus was short: "The fruit of

this genus differs exceedingly from that of *Pancratium* in having only two seeds in each cell which swell to considerable size, like bulbs, and I have named it *Hymenocallis* from the beautiful membrane which connects the filaments." Gradually *Pancratium* has been limited to Europe and *Hymenocallis* to the Americas. However, in 1963 Standley and Steyermark (Fieldiana Bot. 24: 138) used *Pancratium* for all species, noting, "By most recent authors the American species have been treated as a distinct genus, *Hymenocallis*, based upon the number of ovules. This character, however, does not hold, and there being left for segregation of the two genera nothing but their geographic distribution, it seems necessary to unite them, as was done by most of the older workers upon American plants." This action has been followed by Alain (Phytologia 8: 319. 1962), St. John (Mem. Pacific Trop. Bot. Gard. 1: 87. 1973), and Fournet (Fl. Guadeloupe Martinique, 238. 1978). By contrast, Sealey published a "Review of the Genus *Hymenocallis*" (Kew Bull. 1954: 201–240) and an abstract treatment in 1969 (Royal Hort. Soc. Dict. Gard. Suppl. ed. 2. 358–360). Adams (Fl. Pl. Jamaica, 79, 80. 1972) accepted *Hymenocallis*, as has Flory (Nucleus 19: 204–227. 1976), who stated, "*Hymenocallis* has seeds which are comparatively large and fleshy, almost spherical, usually greenish, and few per cell. In comparison, the seeds of *Pancratium* are usually black, flattish — but sometimes angular, more numerous per cell, and stacked." *Hymenocallis* is accepted for the *Flora of the Lesser Antilles*.

Hymenocallis arenicola Northrop, Mem. Torrey Bot. Club 12: 29. 1902.

Described from the Bahamas, this species has been a problem ever since its publication. Stehlé (Fl. Agron. Antill. Fr. 3: 162–165. 1960; Bull. Soc. Bot. France 123: 446. 1976) recognized both *Hymenocallis caribaea* and *H. arenicola* for Martinique and Guadeloupe. The former, he stated, grows on humus or laterite areas and has oblong petals, while the latter occurs on sandy areas and has linear and narrow petals. Fournet (Fl. Guadeloupe Martinique, 238. 1978) reported the species to be very similar, differing in leaf apex and tepal width. No specimens have been seen, and the illustrations supplied by Stehlé are inadequate, suggesting not even the typical *H. caribaea* but *H. fragrans* instead.

Britton and Millspaugh (Bahama Fl. 78. 1920) considered *Hymenocallis arenicola* a synonym of *H. declinata* (Jacq.) Roemer. León (Fl. Cuba 1: 315. 1946) recognized *H. arenicola* and *H. caribaea* (L.) Herb. and cited *H. declinata* in the synonymy of the latter but failed to give characteristics to distinguish the species. Sealey (Kew Bull. 1954: 226. 1954) recognized *H. arenicola* but cited only material from the Bahamas. He, too, included *H. declinata* in the synonymy of *H. caribaea*. Adams (Fl. Pl. Jamaica, 80. 1972) referred to *H. arenicola* as "an obscure species, the Jamaican plants thus identified not being clearly distinct from *H. caribaea*." In 1976 Flory (Nucleus 19: 204–227) listed chromosome num-

bers for *H. caribaea* from commercial and California sources with complements of $2n = 46$; material of *H. arenicola* from Jamaica had $2n = 48$, and from the Bahamas, counts of $2n = 48$ and $2n = 50$.

Hymenocallis caribaea (L. emend. Ker-Gawler) Herbert, Bot. Register 7(app.): 44. 1821.

The basionym is *Pancratium caribaeum* L. (Sp. Pl. 291. 1753). Sealey (Kew Bull. **1954**: 218–222. 1954) discussed the typification of this species, noting that no herbarium specimens validating the name existed and that the references cited by Linnaeus represented several species. A Commelin reference (Horti Med. Amstelod. Rar. Pl. Descr. Ic. **2**: 173. *t. 87*. 1701) was cited by Ker-Gawler in publishing a new description along with a plate (Curtis's Bot. Mag. **21**: *t. 826*. 1805). The lectotype is the Commelin illustration, with a more modern reference of Curtis's *t. 826*.

Adams (Fl. Pl. Jamaica, 80. 1972) has suggested, "*H. caribaea* and *H. fragrans* may not be distinct. Difference in the shape of the leaf-bases may depend on the size of the bulb. In those plants of *Hymenocallis* in which the pedicel is short, thick and almost indistinguishable from the ovary in the flowering stage, there is a tendency as the fruit develops for the pedicel to elongate and become slender so that a definite fruit-stalk is formed which may even allow the ripe fruit to become pendulous." Although Sealey's treatment is adopted for the plants from the Lesser Antilles, I concur that only specimens representing the extremes of variation are clearly separable.

Hymenocallis humilis S. Watson, Proc. Am. Acad. **14**: 301. 1879; Garden Forest 1: 14. 1888.

A specimen *Duss 4210* (NY), cultivated on Guadeloupe in 1905, may be referred to this species. Sealey (Kew Bull. **1954**: 238. 1954) did not see material of this species but accepted it, suggesting that it might be conspecific with *Hymenocallis palmeri* or nothing more than a young offshoot of *H. rotata*.

Zephyranthes atamasco (L.) Herbert, Bot. Register 7(app.): 36. 1821.

Duss (Fl. Phan. Antill. Fr. 562. 1897) reported *Amaryllis atamasco* L. in cultivation in the two French colonies and cited his own collection *3315b*. Fournet (Fl. Guadeloupe Martinique, 234. 1978) repeated this record without indicating current cultivation. Neither the Duss collection nor other, more recent collections have been seen.

Zephyranthes citrina Baker, Curtis's Bot. Mag. **108**: *t. 6605*. 1882.

The name *Zephyranthes aurea* Baker (Handb. Amaryllid. 37. 1888) has been used by Questel (Fl. St. Barts, 90. 1941), Stehlé (Bull. Soc. Bot. France 123: 446. 1976), and Fournet (Fl. Guadeloupe Martinique, 234.

1978) for the weedy, yellow-flowered *Zephyranthes* of the Lesser Antilles. The combination *Zephyranthes aurea* (Ruiz & Pavon) Baker (basionym: *Amaryllis aurea* Ruiz & Pavon, Fl. Peruv. Chil. 3: 56. *t. 286a.* 1802) was illegitimate when published for two reasons. First, included in the synonymy by Baker was *Amaryllis tubiflora* L'Hér. Sertum Angl. 10. 1788, which should have been used as the basionym. According to Macbride (Publ. Field Mus. Bot. 13(1): 668. 1936), *Zephyranthes tubiflora* (L'Hér.) Schinz is the correct name for the Peruvian species. Second, predating the combination by Baker is *Zephyranthes aurea* S. Watson (Proc. Am. Acad. 18: 161. 1883), a species from Arizona and Mexico. The Watson name was placed in the synonymy of *Z. longifolia* Hemsley by Coulter (Contr. U. S. Natl. Herb. 3: 133. 1894).

Zephyranthes grandiflora Lindley, Bot. Register 11: 902. 1825.

With the original description Lindley cited *Amaryllis minuta* H.B.K. Nov. Gen. Sp. 1: 278. 1816, and Kunth, Synopsis Pl. 1: 285. 1822. I cannot find the binomial *Amaryllis minuta* used in modern publications, and a new combination may be required, a task I leave to the specialists working on the family.

Zephyranthes puertoricensis Traub and **Z. tubispatha** Herbert

In recent publications, Sealey (Curtis's Bot. Mag. n.s. 170: *t. 232.* 1954) and Traub (Taxon 7: 109–113. 1958) both acknowledge that *Amaryllis tubispatha* L'Héritier (Sertum Angl. 9. 1788) was based on a red-flowered plant from Argentina collected by Commerson. Further, both recognize that this taxon differs from the white-flowered species from Jamaica commonly known as *Zephyranthes tubispatha* Herbert (Bot. Register 7(app.): 36. 1821, based on *Amaryllis tubispatha* sensu Ker-Gawler, Curtis's Bot. Mag. 38: *t. "1568."* 1813). Sealey regarded *Z. tubispatha* Herbert as a new name applicable to the white-flowered plants; however, he did not rename the red-flowered plants from Argentina. Although Herbert did not cite the L'Héritier name, he did make reference to Curtis's Bot. Mag. *t. "1568"* (correctly *1586*) where Willdenow's *Species Plantarum* 2: 51 is cited in synonymy; the latter publication also includes a reference to the original Commerson collection. Thus, as Traub indicated, by application of Article 55f of the *International Code of Botanical Nomenclature*, the correct name for the red-flowered plants from Argentina is *Zephyranthes tubispatha* (L'Hér.) Herbert ex Traub. The type of this name cited by L'Héritier is *Commerson 3116*, from Buenos Aires, Argentina (P).

Traub had previously renamed the white-flowered plant *Zephyranthes puertoricensis* Traub (Pl. Life 7: 37. *fig. 4a.* 1951) and concluded that the misnamed Ker-Gawler plant had to be included under this name. He designated *Traub 151* (TRA) as holotype (Taxon 7: 111. 1958); clearly this should have been a neotype, but the choice of a neotype seems ill-advised, when Curtis's Bot. Mag. *t. 1586*, the basis of the new name, could have been designated lectotype.

COMMELINACEAE

Leptorrhoeo Clarke in Hemsley

The Central American genus *Leptorrhoeo* is to be included in the flora of the Lesser Antilles as a result of two weedy specimens from a population persisting on the island of St. Lucia. Determining the correct name for this plant presented several problems. The data for the genus *Leptorrhoeo* in the *Index Nominum Genericorum* lead one to conclude that the genus and the type species are both illegitimate. The citation is "*Leptorhoeo* C. B. Clarke in Hemsley Diagn. Pl. Nov. 55. 1880. Type species: *L. filiformis* C. B. Clarke, nom. illeg. (*Commelina floribunda* H.B.K.) = *Descantaria* Schlechtendal 1853." Handlos has clarified these problems in an abbreviated manner in his monograph of *Tripogandra* (Rhodora 77: 213–333. 1975); however, further explanation seems desirable.

Leptorhoeo was published by Clarke in Hemsley's work with a single species, *L. filiformis* (Martens & Gal.) Clarke. Clarke cited the basionym *Tradescantia filiformis* Martens & Gal. Bull. Acad. Bruxelles 9: 376. 1842, and a synonym, *Aneilema floribunda* Hooker & Arnott, Bot. Beechey Voy. 311. 1841. The latter reference has been the source of confusion in several genera and should be excluded from *Leptorhoeo*. The type specimen is *Galeotti 4957* from Oaxaca, Mexico, as cited by Clarke.

In treating the plants collected by Captain Beechey in Mexico, Hooker and Arnott (*ibid.*) stated, "*Aneilema floribunda*. *Commelina floribunda* H.B.K., Nov. Gen. Am. 1, p. 269" without giving any description or citing any collection. Baillon (Hist. Pl. 13: 218. 1894) regarded "*Aneilema floribunda* Hook. & Arn." as a new name and transferred the species to *Leptorhoeo*. Apparently Woodson concurred when he published *Tripogandra floribunda* (Hooker & Arn.) Woodson (Ann. Missouri Bot. Gard. 29: 152. 1942) and (*ibid.* 31: 146. 1944) when he listed *Tradescantia filiformis* Martens & Gal., *Leptorhoeo filiformis* (Martens & Gal.) Clarke, and *Leptorhoeo floribunda* (Hooker & Arn.) Baillon in synonymy. Rodweder (Abh. Auslandsk. 61: 152. 1956) accepted *Leptorhoeo* with the single species *L. floribunda* (Hooker & Arn.) Baillon, and with *L. filiformis* in synonymy.

In his monograph of *Tripogandra* (Rhodora 77: 213–333. 1975), Handlos stated (p. 286), "Hooker and Arnott published the combination *Aneilema floribunda* based on *Commelina floribunda* HBK., but the specimen to which they applied this name was a species of *Leptorhoeo*, a genus in need of further study." Handlos must have drawn this conclusion from a Beechey specimen cited by Clarke but not by Hooker and Arnott. The name *Commelina floribunda* HBK. (Nov. Gen. Sp. 1: 260. 1815) is typified by a Humboldt and Bonpland specimen from Cumana, Bordones, and Quetepe. Handlos assigned *Commelina floribunda* HBK. to the synonymy of *Tripogandra multiflora* (Sw.) Raf., which is the type species of the genus *Tripogandra* and is based on *Tradescantia multiflora* Sw. (Prodr. 57. 1788). Thus *Aneilema floribunda*, *Leptorhoeo floribunda*, and *Tripo-*

gandra floribunda, all based on *Commelina floribunda* HBK., must be considered synonyms of *Tripogandra multiflora* (Sw.) Raf., while *Leptorhoeo filiformis* (Martens & Gal.) Clarke is distinct.

The *Index Nominum Genericorum* reference suggests that *Descantaria* Schlechtendal (Linnaea 26: 140. 1853) is an earlier name for *Leptorhoeo* Clarke. As Handlos noted, the name was "proposed for the species which Kunth included in his species anomalae," all of which are considered by Handlos in the genus *Tripogandra*. Schlechtendal did not make any of the combinations. Brückner (Bot. Jahrb. 61: 60, 61. 1926) suggested the specific transfers and later made them (Notizbl. Bot. Gart. Berlin 10: 55–61. 1927; in Engler, Nat. Pflanzenfam. ed. 2. 15a: 171, 172. 1930) but did not designate a type species. The transfer of *Tradescantia filiformis* Martens & Gal. to *Descantaria* was never published. The *Index Nominum Genericorum* cards designate for *Descantaria* "T.: *Tradescantia cumanensis* Kunth, nom. illeg. (*Commelina floribunda* HBK.)." Handlos regarded the following as synonyms of *Tripogandra multiflora* (Sw.) Raf.: *Commelina floribunda* HBK., *Descantaria multiflora* (Sw.) Brückner, and *Descantaria cumanensis* (Kunth) Brückner. Handlos (*op. cit.*, p. 235) also noted the lectotype of *Descantaria* to be *Tradescantia multiflora* Sw. *Descantaria* Schlechtendal is a synonym of *Tripogandra* Raf. and not an earlier name for *Leptorhoeo*.

Although Clarke originally spelled the generic name *Leptorhoeo*, current workers have followed the spelling used by Brenan as *Leptorrhoeo* (Jour. Linn. Soc. Bot. 59: 368. 1966).

Tripogandra Rafinesque, Fl. Tellur. 2: 16. 1837.

Handlos (Rhodora 77: 235. 1975) has stated that the type of *Tripogandra* Raf. is *Tradescantia multiflora* Sw. The *Index Nominum Genericorum* cards designate the type as "*Tripogandra multiflora* Raf. (*Tradescantia multiflora* Jacq. 1790, not Swartz 1788)." Handlos's only comment on this must be taken from the context of his statement that "Rafinesque may have been misled by the apparent though not real differences between Swartz's original description and Jacquin's description and illustration." In citing the basionym of *Tradescantia multiflora* Sw., Handlos included the Jacquin reference (Collect. 3: 226, 227. 1791). He also indicated the type to be "Jamaica. *Swartz* (Holotype, (B)?; isotype, M!)." In the herbarium at Stockholm, there are two sheets of *Tradescantia multiflora* from Jamaica; one of them, with the binomial in Swartz's own hand, should be considered the holotype.

Rafinesque had assigned the Swartz reference to the genus *Heminema* (Fl. Tellur. 2: 17. 1837) and the Jacquin reference to the genus *Tripogandra*. Woodson (Ann. Missouri Bot. Gard. 29: 152. 1942) was the first to combine *Heminema* and *Tripogandra*. He accepted *Tripogandra* and in this is followed by Handlos.

CYCLANTHACEAE

Carludovica gracilis Liebm. and **C. gracilis** Sieber

In describing *Carludovica*, Grisebach (Fl. Brit. W. Indian Is. 513. 1864) included two species occurring in the French islands, one of which was "*C. gracilis*, Liebm. Syn. *C. angustifolia*, Seem. (*Evodianthus* Oerst.), not R. P. *C. Plumieri*, Pl. Carib.: leaves deeply 2-fid, with narrower (1″–1½″ broad) lobes, spathes 3. . . ." This has been recorded as *Carludovica gracilis* Liebm. ex Griseb. and attributed to "Ind. Occ." and Mexico in *Index Kewensis*.

Duss (Fl. Phan. Antill. Fr. 484. 1897) listed "*C. gracilis* Sieb." and cited his own collections. Stehlé (Bull. Soc. Bot. France **123**: 453. 1976) accepted *C. gracilis* Sieber. Harling in his monograph (Acta Horti Berg. **18**: 283. 1958) cited the name *C. gracilis* Liebmann ex Matuda (Anal. Inst. Biol. México **22**: 387. 1952) as a synonym of *Dicranopygium gracile*. He further explained (*ibid.*, pp. 150, 151) that both Grisebach and Duss had incorrectly placed Liebmann's unpublished name on specimens from the French West Indian Islands, collections that should be referred to *Asplundia rigida*. "Sieb." is certainly a misspelling of Grisebach's abbreviation "Liebm." The herbarium specimens identified as *Carludovica gracilis* represent juvenile plants of *Asplundia rigida* with narrow leaf divisions on small leaves; the Lesser Antillean material and the name or names should be referred to *Asplundia rigida* (Aublet) Harling.

HAEMODORACEAE

Xiphidium Aublet, Pl. Guian. 1: 33. 1775.

This generic name is attributed to Loefling (Iter Hisp. 179. 1758) or to Loefling ex Aublet (Pl. Guian. 1: 33. 1775). Loefling cited *Xiphidium* of authors as a synonym of *Ixia*, and Aublet noted this treatment. The genus is correctly attributed to Aublet alone.

HYPOXIDACEAE

Curculigo scorzonerifolia (Lam.) Baker and **Hypoxis decumbens** L.

These names present associated problems in typification. The publication of *Hypoxis decumbens* L. is variously cited as Syst. Nat. ed. 10. **2**: 986. 1759 (May–June, 1759), Pl. Jam. Pugillus, 11. 1759 (December, 1759), Amoenitates **5**: 396. 1759 (September, 1760), and Sp. Pl. ed. 2. **1**: 439. 1762. The earliest publications listed in the *Systema* references are those of Plumier (Pl. Am. *t. 108, fig. 2*, which is a *Curculigo*) and Miller, Fig. Pl. Gard. Dict. *pl. 39, fig. 2* (a *Hypoxis*). The *Pugillus* reference cited only "*Brown. jam. 195*," which appears to represent the specimen preserved in the Linnaean herbarium (LINN *427.2*). In the second edition of *Species Plantarum*, Linnaeus listed the Plumier reference with a

question mark. Thus *Hypoxis decumbens* L. is to be typified by the Browne specimen in the Linnaean herbarium (*427.2*); this is also the plant represented in Miller's *Catalogue Plantarum, pl. 39, fig. 2.* 1730.

The publication of *Curculigo scorzonerifolia* (Lam.) Baker is attributed to Bentham (Fl. Austral. 6: 449. 1873), who indicated the affinity of the American species *Hypoxis scorzoneraefolia* Lam. to *Curculigo* but did not make the combination. Baker (Jour. Linn. Soc. Bot. 17: 124. 1878) published the combination. *Hypoxis scorzoneraefolia* Lamarck (Encycl. Méth. Bot. 3: 183. 1789) should be typified by Plumier, Pl. Am. 99. *t. 108, fig. 2.* Lamarck stated that the plant was collected by Plumier in St. Vincent and Santo Domingo. Although Plumier made no reference to these locations, it is possible that the original drawings in Paris may clarify the exact type locality. The designation of a lectotype for *Hypoxis decumbens* L. removes the problem of the Plumier illustration being cited in the protologue of both species. The Plumier illustration serves as the lectotype of *Hypoxis scorzoneraefolia* Lam.

LEMNACEAE

Britton and Brown (Illus. Fl. No. U. S. ed. 2. 447. 1913) designated *Lemna trisulca* L. as the type species of the genus. Den Hartog and Van der Plas (Blumea 18: 361. 1970) argue against this selection and adopt *Lemna minor* L.

MARANTACEAE

Calathea Meyer, Prim. Fl. Esseq. 6. 1818.

The genus was described by Meyer, who cited the single species *Calathea discolor.* However, *Maranta casupo* Jacq. (Frag. Bot. 51. 1801) was cited in synonymy. Schumann (Engler & Prantl, Pflanzenr. IV. 48: 72. 1902) referred *Maranta casupo* Jacq. and *Calathea discolor* Meyer to the synonymy of *Calathea lutea* (Aublet) Meyer, for which the correct citation should be Meyer ex Korniche in Bull. Soc. Nat. Moscou 35: 114. 1862. The typification of *Maranta lutea* Aublet and *Maranta allouia* Aublet, the basionyms of *Calathea lutea* (Aublet) Meyer ex Koern. and *Calathea allouia* (Aublet) Lindley, respectively, is complicated. No Aublet specimens have been seen or cited in past literature. Aublet did refer to the Plumier manuscript "5, plates 21, 22, 35 and t. 5." These are unpublished plates and are not in the redrawings of the Burman edition.

Ischnosiphon arouma (Aublet) Koern. in Bull. Soc. Nat. Moscou 35: 88. 1862.

The basionym of this name is *Maranta arouma* Aublet, Pl. Guian. 1: 3. 1775, for which the lectotype must be *plate 23* or *24* of Plumier's unpublished manuscript numbered 5.

Maranta gibba J. E. Smith in Rees, Cyclop. Vol. 22 [alph. order], *Maranta* no. 2. 1812.

The occurrence of this species on Antigua was indicated by Grisebach (Fl. Brit. W. Indian Is. 605. 1864) and documented by a Wullschlaegel collection; on Barbados it was reported by Roscoe. The species was originally described from material grown at Liverpool from stock provided by Lord Seaforth when he was governor of Barbados. Seaforth is known to have assembled the plants he sent to Europe from many places in the West Indies and northern South America. It is probable that *Maranta gibba* is not native to Barbados. Schumann (Engler & Prantl, Pflanzenr. IV. **48**: 126. 1902) considered *M. gibba* to be a synonym of *M. divaricata* Roscoe (Monandr. Pl. *t. 27*. 1828), which is later in publication and is based on material from Brazil. Dr. Helen Kennedy has commented to me in correspondence that *M. gibba* is a plant to 2.5 meters tall, quite branched, which flowers in the afternoon. In contrast, *M. arundinacea*, the cultivated arrowroot, is usually under 1 meter tall and less branched; it flowers in the morning. This may help identify the plants described by Stehlé (Bull. Soc. Bot. France **123**: 443. 1976) as *M. arundinacea* and "*M. indica* Tuss." Duss (Fl. Phan. Antill. Fr. 585. 1897) had used the common names "Dictame de la Barbade" and "Moussache de la Barbade" for the plants he also called "*M. indica* Tuss." The collections Duss cited have not been seen but may be referable to *M. gibba*.

Maranta ruiziana Koern. Bull. Soc. Nat. Moscou **35**: 45. 1862.

Two collections, *Duss 4196* and *4472* (both NY), representing plants cultivated in Martinique in 1903, were labeled *Maranta divaricata* but are correctly named *Maranta ruiziana* Koern.

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LARDIZABALACEAE HARDY IN TEMPERATE NORTH AMERICA[1]

S. A. SPONGBERG AND I. H. BURCH

LARDIZABALACEAE Decaisne, Arch. Mus. Hist. Nat. Paris 1: 185. 1839, "Lardizabaleae," nom. cons.

(LARDIZABALA FAMILY)

Erect or usually high-climbing, twining, evergreen or deciduous shrubs, often producing short shoots, the wood frequently with prominent medullary rays. Leaves stipulate (*Lardizabala*) or exstipulate, alternate (sometimes appearing whorled or fasciculate on short shoots), pinnately trifoliolate, palmately compound, ternately decompound, or rarely odd-pinnately compound, the petioles and petiolules articulated; leaflet venation pinnate or usually with 3 major veins from the base. Flowers actinomorphic, perfect, imperfect, or usually imperfect through abortion, arranged in bracteate or ebracteate racemose or paniculate inflorescences, and the plants monoecious, dioecious, androdioecious, or polygamo-dioecious. Perianth 3-merous in 1–4 whorls, inserted hypogynously on a ± well-defined receptacle; calyx comprised of 3–6 free, petaloid sepals in 1 or 2 whorls; corolla sometimes absent[2] or composed of 6 small, free petals or represented by small, petaloid nectaries. Androecium of 6(–8) stamens (in carpellate flowers absent or represented by staminodia), the filaments free or connate into a tube, the anthers free, 2-celled, extrorsely dehiscent by longitudinal slits, the often massive connectives sometimes with elongated apices. Gynoecium apocarpous, of 3–15 conduplicate carpels (in

[1] This treatment of the Lardizabalaceae is the fifth in a series of treatments of cultivated ligneous plants, the preparation of which is a project of the Arnold Arboretum of Harvard University, and the purpose of which is to provide a modern, accurate account of the woody plants encountered in cultivation in the cooler temperate regions of North America. It is hoped that these studies will eventually form the basis for a new manual of cultivated woody plants. The first paper in the series was published in the Journal of the Arnold Arboretum **56**: 1–19. 1975. Reference should be made to the introductory paragraphs of that paper for matters concerning area covered, taxa included, and the general philosophy of these treatments.

Special thanks and gratitude are extended to the Director and trustees of the Stanley Smith Horticultural Trust for a grant that has made possible the illustrations that accompany this treatment. The illustrations are the careful work of Robin S. Lefberg and were prepared from living and alcohol-preserved specimens collected in the Arnold Arboretum and at the Arboretum of the Barnes Foundation, Merion Station, Pennsylvania.

We should also like to acknowledge with deep gratitude the support of the late Mrs. George L. Batchelder, whose gifts to the Arnold Arboretum enabled the initiation of this project and of this series of papers. S. A. S.

[2] By convention, when whorls of the perianth are missing, it is assumed that whorls of the corolla have been suppressed, even if the two whorls of the resultant "calyx" are dimorphic, as in *Decaisnea*.

staminate flowers rudimentary), with conspicuous adaxial sutures and well-defined, sessile stigmas; ovaries unilocular with numerous orthotropous to anatropous or campylotropous (*Lardizabala?*), bitegmic, crassinucellar ovules on laminate placentae or confined to 2 parietal placentae adjacent to the adaxial suture. Fruits ± leathery, yellow, purplish, or blue, thick-walled, many-seeded berries or follicles. Seeds with a hard, shiny, brown or black seed coat, often with a conspicuous basilateral hilum, the small embryo straight, embedded in abundant *ab initio* Cellular endosperm; embryo sac of the Polygonum type. TYPE GENUS: *Lardizabala* Ruiz & Pavon.

A small family of seven or eight genera and upwards of 35 species with a curiously disjunct distribution in temperate regions of eastern Asia from Japan and Korea to the Himalayas (five or six genera) and in South America in Chile (two genera). Species of only two genera, *Akebia* and *Decaisnea*, are known to be grown within our range. However, in warmer temperate areas of North America, species of *Lardizabala* Ruiz & Pavon (two evergreen, dioecious species of Chile with stipulate, ternately decompound leaves), *Stauntonia* DC. (ca. six deciduous, monoecious species of eastern Asia with palmately compound leaves and staminate flowers with the stamens monadelphous), *Holboellia* Wallich (ten evergreen species of the Himalayan region and China with palmately compound leaves and flowers with 6 sepals, the petals absent), and *Sinofranchetia* (Diels) Hemsley (one species, *S. chinensis* (Franchet) Hemsley, of central and western China with pinnately trifoliolate leaves and flowers with 6 sepals and 6 nectariferous petals) are known or thought to be cultivated.

It should also be noted that *Sargentodoxa cuneata* (Oliver) Rehder & Wilson, Pl. Wilsonianae 1: 350. 1913, a taxon closely related to and once included in the Lardizabalaceae but subsequently removed to its own family, Sargentodoxaceae Stapf ex Hutchinson, Fam. Fl. Pl. 1: 100. 1926; Bot. Mag. **151**: *tt. 9111, 9112*. 1926, was treated by Rehder in his *Manual* (1940) and his *Bibliography* (1949). However, we have found no evidence in the literature, in collection inventories, or in herbarium records of its current cultivation in North America.

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Key to the Genera of Lardizabalaceae in Cultivation

1. Twining shrubs; leaves pinnately trifoliolate and/or palmately compound; sepals (2), 3, 4, (or rarely to 6); stamens free. ..... 1. *Akebia*.
1. Erect shrubs with several stems from the base; leaves large, with numerous leaflets, odd-pinnately compound; sepals 6; stamens monadelphous. ..... 2. *Decaisnea*.

1. Akebia Decaisne, Compt. Rend. Acad. Sci. Paris **5**: 394. 1837; Arch. Mus. Hist. Nat. Paris **1**: 195. 1839.

Glabrous, deciduous or occasionally evergreen, twining shrubs from fibrous roots, sometimes of rampant growth; stems silver-tan or grayish, lenticellate, the pith white, small, continuous; winter buds ovoid, with numerous imbricated, often persistent scales. Leaves exstipulate, on long, basally articulated petioles, alternate on new growth and/or appearing fascicled from short shoots on old growth, pinnately trifoliolate and/or palmately compound with 4, 5, (or to 7) leaflets, the leaflets on distally and proximally articulated petiolules; blades ± subcoriaceous, oblong-ovate to elliptic, or obovate, with truncate to cuneate bases, entire, sinuate, or shallowly lobed, often undulating margins, and retuse and inconspicuously mucronate apices; venation pinnate with 3 major veins from the base. Flowers functionally unisexual (and the plants functionally monoecious), on basally articulated pedicels in axillary, bracteate, pendent racemes appearing with the leaves in spring from short shoots on old growth; staminate flowers clustered apically on short pedicels, the carpellate flowers long-pedicellate, inserted toward or at the base of the raceme (or occasionally absent). Sepals (2), 3, 4, (or rarely to 6), free, concave and ± ovate. Corolla absent. Stamens 6(–8), free, in staminate flowers the anthers incurved over a rudimentary gynoecium and dehiscing extrorsely; in carpellate flowers minute vestigial stamens usually alternating with the carpels at the base of the gynoecium. Gynoecium apocarpous, the (3–)5–8(–15) conduplicate carpels cylindrical, with prominent, grooved adaxial sutures extending to the center of the large, sessile stigmatic crests, the stigmas secreting a sticky exudate; ovary unilocular with numerous ovules on laminate placentae. Fruits purplish or bluish, leathery, thick-walled follicles dehiscent along the adaxial suture, exposing the numerous seeds embedded in whitish, gelatinous placental tissue. Seeds ovoid to ± spindle shaped, with a shining black or dark reddish brown seed coat and a conspicuous basilateral hilum; endosperm copious, surrounding the small, straight embryo. (*Rajania* Houttuyn, non L.) Lectotype species: *A. quinata* (Houttuyn) Decaisne; see A. Rehder, Bibliogr. Cult. Trees Shrubs, 166. 1949. (Name adapted from the Japanese name for the plant.) — Akebia.

Four species, two widely distributed in eastern Asia in Japan, Korea, and China, *A. chingshuiensis* T. Shimizu, endemic to Taiwan, and *Akebia longeracemosa* Matsuma, known from Taiwan and central China (Hunan Province). The two widely distributed species, *A. quinata* and *A. trifoliata*, are known in cultivation, while a naturally occurring hybrid between them, *A.* × *pentaphylla*, is also grown in North America. Neither *A. longeracemosa* nor *A. chingshuiensis* is known to us in cultivation.

While akebias in cultivation are commonly seen to flower, fruiting has been reported to be uncommon. At the Arnold Arboretum, however, quantities of fruit have been produced, both as a result of artificial interspecific pollinations and, in other years, without artificial pollinations. Because the plants observed fruiting without artificial pollinations are grown in close proximity on the same arbor, it would appear that cross-pollination (either inter- or intra-specific) is required for fertilization. This hypothesis is given indirect support since other, isolated akebia plants at the Arboretum have not been seen to set fruit.

In Japan, the leathery follicles are sometimes sold in markets as comestibles, while the long, twining stems are used to make wicker items.

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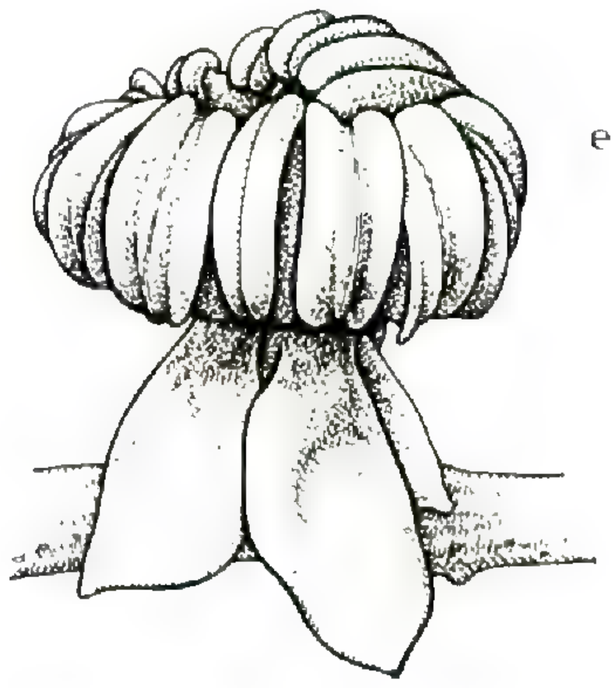
KEY TO THE TAXA OF AKEBIA IN CULTIVATION

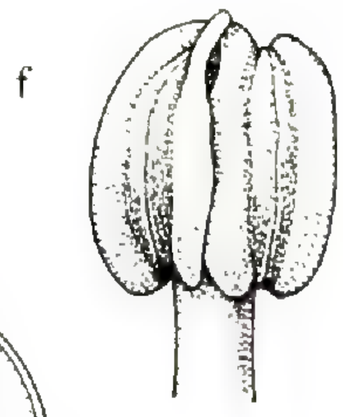
1. Leaves 5-, 4-, and/or 3-foliolate; leaflet blades widest at or below the middle; pedicel of 1 carpellate flower of an inflorescence often inserted at the base of the raceme; staminate flowers on pedicels 1–7 mm. long. ..... 2.
   2. Leaves generally pinnately trifoliolate, the leaflet blades widest below the middle; flowers odorless; carpellate flowers hanging above the cluster of staminate flowers; staminate flowers on pedicels 2–4(–6) mm. long, at anthesis appearing sessile. ..... 1. *A. trifoliata.*
   2. Leaves palmately compound with 4 or 5 leaflets or occasionally pinnately trifoliolate, the leaflet blades widest at or below the middle; flowers faintly fragrant; carpellate flowers hanging above to slightly below the cluster of staminate flowers; staminate flowers on pedicels 4–7 mm. long, not appearing sessile at anthesis. ..... 3. *A.* × *pentaphylla.*
1. Leaves generally 5-foliolate; leaflet blades widest above the middle; pedicels of carpellate flowers inserted on the peduncle above the base of the raceme; staminate flowers on pedicels (3–)9–15 mm. long. ..... 2. *A. quinata.*

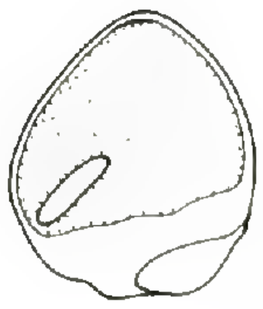
1. **A. trifoliata** (Thunberg) Koidzumi, Bot. Mag. Tokyo **39**: 310. 1925.

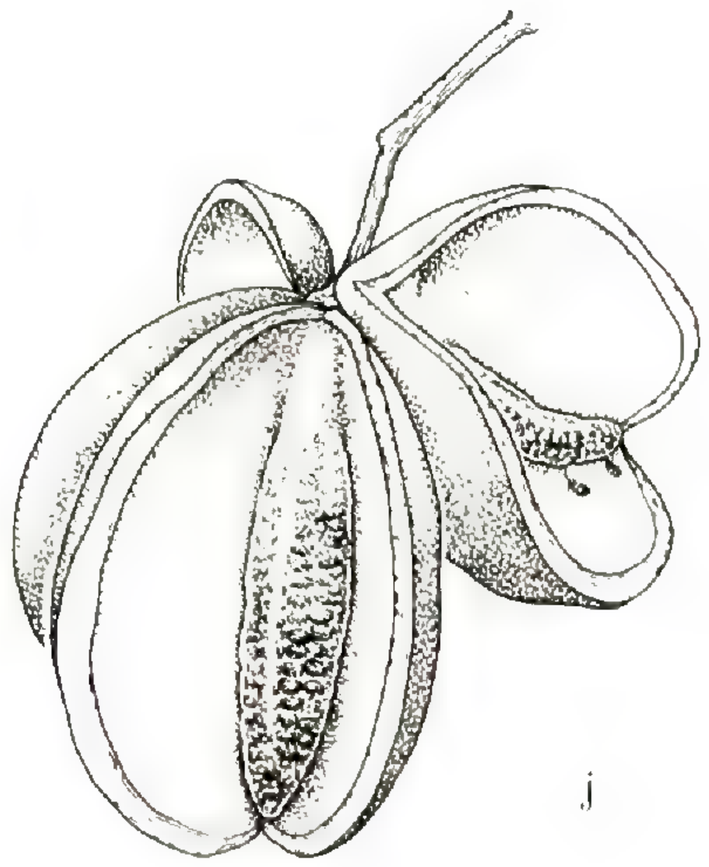
FIGURE 1, d–h.

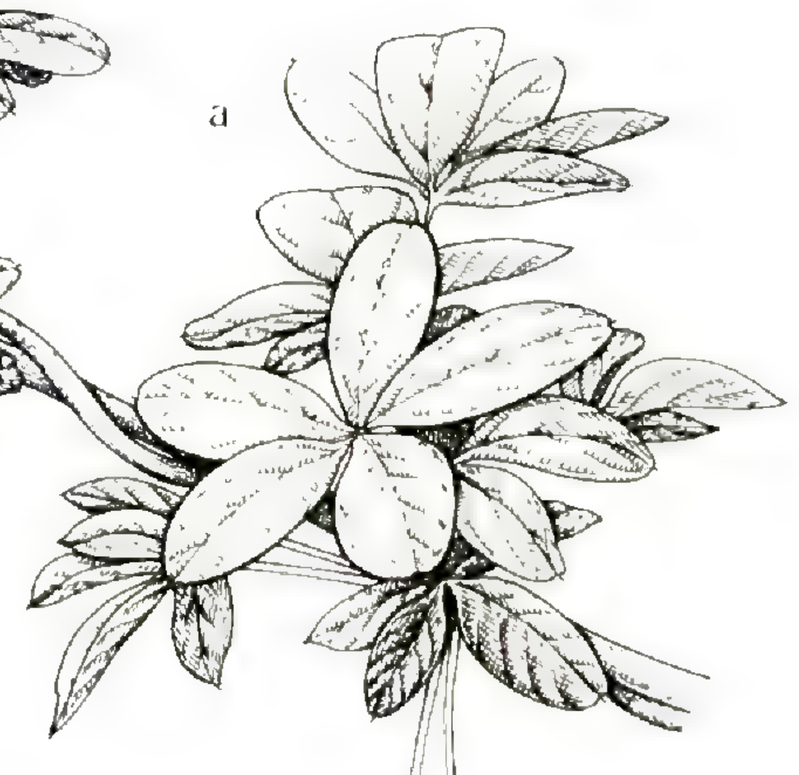
Vigorous twining shrubs, the branches slender, with tan or silvery to purplish brown bark and numerous, often raised, tannish lenticels; winter buds ovoid, ca. 5 mm. long, with 12–15 reddish brown, imbricated scales. Leaves pinnately trifoliolate (or rarely with 4 leaflets and palmately compound), sometimes persistent into winter (and occasionally the plants evergreen), usually turning black and dropping in fall; petioles (1.7–)3–9(–13.5) cm. long; petiolules 0.6–4.5 cm. long, the 2 lateral petiolules usually shorter than the terminal one; terminal leaflets (2.2–)4.2–9.7(–10.3) cm. long, 4–7 cm. wide, the lateral leaflets usually slightly smaller and subequal, the blades oblong-ovate to broadly ovate or sometimes ± rhombic or suborbicular, with cuneate to truncate or cordate bases, irregularly sinuate to shallowly and irregularly lobed or entire margins, and rounded to retuse and inconspicuously mucronate apices; upper surfaces of the blades dark green, the lower surfaces pale green, occasionally ± glaucous. Flowers odorless, in pendent, axillary racemes 7–13 cm. long. Staminate flowers numerous (ca. 7–20), on short, basally bracteate, articulated pedicels 2–4(–6) mm. long; sepals 3, dark reddish purple, 2.5–3 mm. long, ovate to suborbicular, concave and reflexed at anthesis; stamens 6, 7, or 8, dark reddish purple, 2.5–3.5 mm. long, incurved over the rudimentary gynoecium. Carpellate flowers 2 or 3 (or occasionally lacking), borne on basally bracteate and articulated peduncle-like pedicels 1.2–3.6 cm. long toward or at the base of the inflorescence; sepals 3–6,

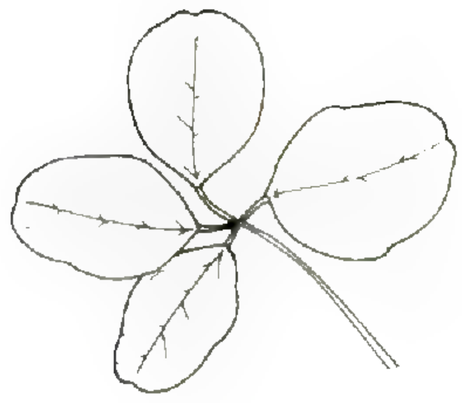


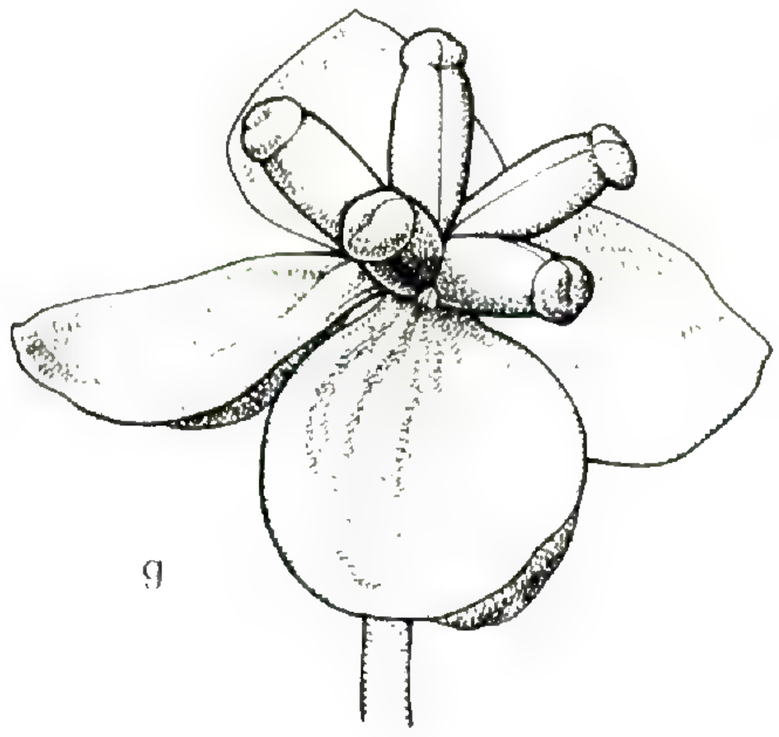


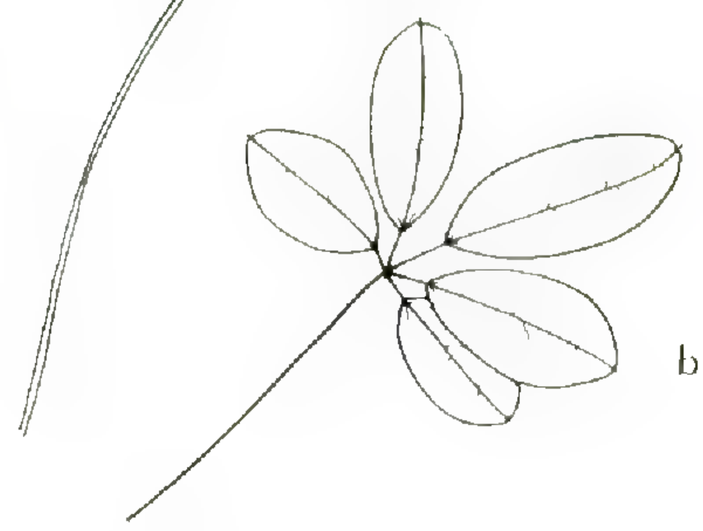












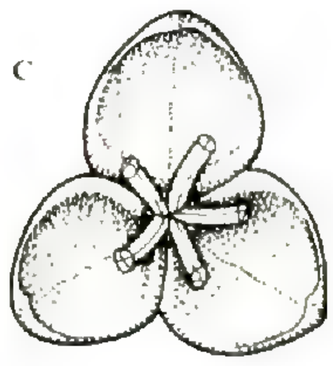


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FIGURE 1. **Akebia.** a–c, *A. quinata*: a, habit of a portion of twining stem with pendulous racemes, × 1/2; b, outline of typical leaf with 5 leaflets, × 1/2; c, carpellate flower, × 1. d–h, *A. trifoliata*: d, outline of typical pinnately trifoliolate leaf, × 1/2; e, staminate flower with reflexed sepals, × 6; f, dehisced stamen, × 18; g, carpellate flower with 4 sepals, × 3; h, longitudinal section through conduplicate carpel, × 6. i–l, *A.* × *pentaphylla*: i, outline of leaf with

dark reddish purple, 6–8(–15?) mm. long, broadly ovate to suborbicular, acute to rounded at the apices, strongly concave and spreading to reflexed at anthesis; androecium rudimentary, the minute stamens equal to or fewer than and alternating with the carpels; carpels 5–8(–15), dark reddish purple, (3–)4–6 mm. long. Fruits borne on the ± woody, accrescent pedicels, initially green, pale violet to bluish with small white dots at maturity, oblong in outline, 5–8 cm. long, longitudinally dehiscent; seeds dark reddish brown, ca. 6 mm. long, ± ovate in outline with a ± acute apex and a conspicuous basilateral hilum. $2n = 32$. (*Clematis trifoliata* Thunberg, *Akebia lobata* Decaisne, *A. quercifolia* Siebold & Zuccarini, *A. clematifolia* Siebold & Zuccarini, *A. sempervirens* Nakai; including *A. trifoliata* var. *australis* (Diels) Rehder, *A. trifoliata* var. *integrifolia* T. Shimizu, and *A. trifoliata* var. *honanensis* T. Shimizu.) — THREE-LEAFLET AKEBIA.

Widely distributed in eastern Asia in China and Japan. (See *distribution map 79* in Y. Horikawa, Atlas of the Japanese flora, an introduction to plant sociology of East Asia. 12 pp. + *500 maps* + viii pp. + *map in pocket*. Tokyo. 1972, for distribution in Japan.) This species is apparently quite rare in cultivation in North America. The one accession of *Akebia trifoliata* now growing in the Arnold Arboretum (AA #12659, of cultivated origin) is undoubtedly the plant used by Sax (see Anderson, 1934, 1935) in cross-pollinations with *A. quinata* in the successful synthesis of the hybrid *A.* × *pentaphylla*. The Arboretum plant of *A. trifoliata*, and others from cultivation represented in the herbarium at AAH, have the leaflets with nearly entire margins and thickly coriaceous, oblong-ovate blades.

Akebia trifoliata is an exceedingly variable species in nature and, according to Shimizu's (1961) classification, consists of two subspecies, subsp. TRIFOLIATA and subsp. AUSTRALIS (Diels) Shimizu, Quart. Bull. Taiwan Mus. 14: 201. 1961, that differ in size of carpellate flowers. The typical subspecies has flowers less than 2 cm. in diameter, while in subsp. AUSTRALIS the carpellate flowers are recorded as ranging from 2 to 4 cm. in diameter. Shimizu further subdivides each subspecies into two varieties on the basis of ± entire (subsp. TRIFOLIATA var. INTEGRIFOLIA T. Shimizu and subsp. AUSTRALIS var. AUSTRALIS T. Shimizu) versus sinuate or lobed (subsp. TRIFOLIATA var. TRIFOLIATA and subsp. AUSTRALIS var. HONANENSIS T. Shimizu) leaflet margins.

After examining specimens at A and GH collected from the wild, however, we are hesitant to accept this infraspecific classification. While certain specimens appear distinctive in leaf characters, the variation in these characters forms a continuum, and some individual specimens exhibit wide extremes of variation. Specimens at one extreme have entire-margined, coriaceous, reticulate, ovate to oblong-ovate leaflets from evergreen or deciduous plants, while specimens from the more usual deciduous plants

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4 leaflets, × 1/2; j, habit of 3 follicles (from 1 flower) on the accrescent, woody pedicel, × 1/3; k, seed, × 1 1/2; l, longitudinal section through seed showing embryo and endosperm (stippled), × 4.

have ovate to broadly ovate, thinly coriaceous, weakly reticulated leaflets with sinuate margins. Plants corresponding to the first-described variant have been segregated as var. AUSTRALIS (Diels) Rehder, Jour. Arnold Arb. 10: 189. 1929, and Rehder (Man. Cult. Trees Shrubs, ed. 1. 231. 1927) attributed a larger carpellate flower diameter to this variety. However, flower diameter does not appear to be correlated with the foliage characters. As a result, it does not seem possible (or desirable) to define or adopt previously recognized infraspecific taxa within *Akebia trifoliata* without data from a detailed study of this species throughout its range. In this connection, Anderson (1935) has speculated that plants referred to *A. trifoliata* var. AUSTRALIS may represent plants of *A.* × *pentaphylla* that have introgressed with *A. trifoliata* through backcrosses with that parent.

2. **A. quinata** (Houttuyn) Decaisne, Arch. Mus. Hist. Nat. Paris 1: 195. 1839. FIGURE 1, a–c.

Deciduous, high-climbing, twining shrubs with gray to silvery or rosy-gray, lenticellate bark on old shoots, the slender young shoots reddish brown; winter buds acute, ca. 6 mm. long, with numerous reddish brown, imbricated scales. Leaves palmately 5-foliolate (or occasionally some leaves with 4, 6, or 7 leaflets); petioles 4–14.3 cm. long; petiolules 0.5–2.5 cm. long; terminal (middle) leaflets 4–7 cm. long, 1–3.5(–4.9) cm. wide, the 2 pairs of lateral leaflets each slightly reduced in size, the leaflets of a pair subequal; blades thinly coriaceous, oblong to oblong-obovate or elliptic with cuneate to obtuse bases, entire, often undulating margins, and rounded to shallowly retuse and inconspicuously mucronate apices; upper surfaces of the blades dark green, the lower surfaces pale green, sometimes ± glaucous. Flowers fragrant, in pendent, axillary racemes 4.5–9(–12) cm. long. Staminate flowers numerous (4–15), on basally bracteate, articulated pedicels (3–)5–9(–15) mm. long; sepals 3, purple to pinkish lavender, 5–8(–9) mm. long, ovate to ± elliptic, strongly concave and reflexed at anthesis; stamens 6 or 7, purplish black, 4–5 mm. long, incurved over the rudimentary gynoecium. Carpellate flowers 1–3 (or occasionally lacking), borne on peduncle-like, basally bracteate pedicels 3–5.5 cm. long toward the base of the raceme; sepals 3 or 4, reddish purple, 0.9–1.5 cm. long, ovate to suborbicular, usually ± acute at apex, spreading at anthesis; androecium of minute, vestigial stamens alternating with the carpels; carpels 5–7, bluish purple, the capitate stigmas reddish purple. Fruits borne on the ± woody, accrescent pedicels, the follicles initially green, becoming purplish with small white dots at maturity, oblong, 6.4–9 cm. long, the leathery walls ca. 4 mm. thick; seeds numerous, reddish brown to black, ca. 6 mm. long, ovoid, ± acute at apex and with a conspicuous basilateral hilum. $2n = 32$. (*Rajania quinata* Houttuyn, *Akebia micrantha* Nakai; including *A. quinata* var. *polyphylla* Nakai.) — FIVE-LEAFLET AKEBIA.

Widely distributed in eastern Asia in China, Japan, and Korea. (See *distribution map 78* in Y. Horikawa, *op. cit.*, for distribution in Japan and

portions of Korea and China.) *Akebia quinata* is not infrequently cultivated in North America and has been reported as naturalized in Massachusetts, Pennsylvania, Michigan, and North Carolina. In nature and when escaped from cultivation, the plants often form large colonies that totally blanket shrubs and small trees; due to this rampant growth some authors have cautioned that *A. quinata* may become a noxious weed, invasive and harmful to native vegetation.

Plants of *Akebia quinata* producing carpellate flowers with six rather than three or four sepals have been segregated as f. *diplochlamys* (Makino) T. Shimizu, Quart. Jour. Taiwan Mus. **14**: 202. 1961 (*A. quinata* var. *diplochlamys* Makino, Jour. Jap. Bot. 7: 376. 1931; *ibid.* **8**: 6. 1932), while other variants producing greenish to whitish flowers [3] have been described as f. *viridiflora* Makino, Bot. Mag. Tokyo **16**: 182. 1902 (*A. quinata* var. *yiehi* W. C. Cheng, Contr. Biol. Lab. Sci. Soc. China **8**: 289. 1933). Although we are unaware of either of these variants as cultivated plants in North America, the white-flowered plants are apparently cultivated in Japan and may be available from Japanese nursery firms.

3. **A. × pentaphylla** (Makino) Makino, Bot. Mag. Tokyo **16**: 30. 1902. [*Akebia quinata* × *A. trifoliata.*] FIGURE 1, i–l.

Vigorous twining shrubs, similar in most characters to *Akebia trifoliata*, intermediate between that species and *A. quinata* in others. Leaves variable, on petioles 4–12.5 cm. long, pinnately trifoliolate or 4- or usually 5-foliolate and palmately compound (rarely with 6 or 7 leaflets); leaflet blades 3.5–10.7 cm. long, 2.5–6 cm. wide, ovate to oblong-ovate or elliptic with entire to sinuate and often undulating margins and rounded to obtuse and inconspicuously mucronate apices; upper surfaces of the blades dark green, the lower surfaces lighter green, sometimes ± glaucous. Flowers faintly fragrant, in pendulous, axillary racemes 9–13 cm. long. Staminate flowers numerous, on short, basally bracteate, articulated pedicels 4–7 mm. long; sepals 3, dark reddish- to blackish-purple, 3–4.5 mm. long, ovate to suborbicular, strongly concave and reflexed at anthesis; stamens 6, dark reddish purple, 2.5–3.5 mm. long, incurved over the rudimentary gynoecium. Carpellate flowers 1–3 (or occasionally lacking), borne on basally bracteate and articulated peduncle-like pedicels (1.9–)2.7–5.7 cm. long inserted toward or at the base of the raceme; sepals 3 or 4, dark reddish- or blackish-purple, 7–11 mm. long, suborbicular with a ± acute apex, spreading to reflexed at anthesis; androecium rudimentary, the stamens minute, equal to and alternating with the carpels; carpels 6, 7, or 8, dark reddish purple, each 5–6 mm. long at anthesis, terminated by a distinct capitate stigma. Fruits initially green, becoming rosy purple, surface

[3] Specimens of white-flowered plants of *Akebia* at A from Japan have been annotated with an unpublished varietal epithet (*leucantha*) attributed to Nakai, which we have been unable to locate in Nakai's published writings. Moreover, a plant growing at the Arnold Arboretum (AA #2033–65) was received under another varietal epithet (*rosea*) to which we have also been unsuccessful in locating a published reference.

with white dots, oblong, (5.2–)6.1–9.1 cm. long, leathery, longitudinally dehiscent; seeds black, ovoid, 4–6 mm. long, with a conspicuous basilateral hilum. $2n = 32$. (*Akebia lobata* β *pentaphylla* Makino; including *A.* × *pentaphylla* var. *integrifolia* Y. Kimura.)

Apparently widely distributed in Japan, where it undoubtedly occurs with both parents (cf. Makino, 1902). Rare in western gardens, *Akebia* × *pentaphylla* might be expected if both *A. quinata* and *A. trifoliata* are grown in close association and their seeds are sown. Seeds, from which plants of this taxon were established at the Arnold Arboretum, resulted from intentional cross-pollinations between the parental species (see Anderson, 1934; Anderson & Rehder, 1935).

Plants of *Akebia* × *pentaphylla* producing carpellate flowers with six rather than three or four sepals have been recognized as f. *diplochlamys* (Nakai) T. Shimizu, Quart. Jour. Taiwan Mus. 14: 202. 1961 (*A.* × *pentaphylla* var. *diplochlamys* Nakai in Matsumura, Ic. Pl. Koisikavenses 4: 103. *pl. 264.* 1921), but we have no evidence of this variant in cultivation in North America.

2. Decaisnea J. D. Hooker & T. Thomson, Proc. Linn. Soc. London 2: 350. 1854; Fl. Indica, 212. 1855, nom. cons.

Erect, deciduous shrubs of araliaceous appearance, the brittle branches longitudinally striate, silvery to yellowish- or greenish-tan with conspicuous lenticular lenticels and large leaf scars; pith large, white, continuous; winter buds with 2 outer scales. Leaves exstipulate, alternate, odd-pinnately compound with 13, 15, or 17 leaflets, the petiole articulated at base and petiolules articulated on the rachis at the insertion of the leaflets (these articulations not clearly evident on new growth or until dried); leaflet blades membranaceous, ovate to elliptic with attenuate to obtuse bases, entire margins, and acuminate apices, the venation pinnate. Flowers on short pedicels, arranged in elongated, bracteate racemes (the racemes often forming panicles) terminating lateral branches; flowers bisexual and functionally perfect or functionally staminate and the plants androdioecious or occasionally polygamo-dioecious with both functionally staminate and perfect flowers on different branches of the panicle or in different racemes. Sepals 6, dimorphic, the outer whorl of 3 narrow, ± subulate, long-acuminate, the inner whorl of 3 lanceolate, strongly keeled. Stamens 6, in staminate flowers with the filaments connate, forming a tube, the free anthers dehiscing extrorsely by longitudinal slits; in perfect flowers the staminal tube short and the stamens ± free. Gynoecium apocarpous, the 3 carpels cylindrical, in staminate flowers rudimentary and included within the staminal tube, the stigmas not developed; in perfect flowers the carpels exserted from the staminal tube, each terminated by a conspicuous, flaplike or knoblike stigma with a prominent groove continuous with the adaxial suture of the carpel wall; ovary unilocular with numerous ovules on 2 parietal placentae adjacent to the adaxial suture. Fruit a cylindrical,

± straight to strongly recurved, leathery, thick-walled, blue, indehiscent berry or yellow, dehiscent follicle. Seeds numerous, arranged in 2 rows and embedded in a white, aril-like pulp emanating from the carpel wall, the seeds flattened, ± oblong to rounded in outline, the seed coats brown or black; embryo small, straight, embedded in copious endosperm. (*Slackia* W. Griffith, 1848; not W. Griffith, 1851 or W. Griffith, 1854.) TYPE SPECIES: *D. insignis* (W. Griffith) J. D. Hooker & T. Thomson. (Name honoring Joseph Decaisne, 1807–1882, Belgian botanist, one-time director of the Jardin des Plantes, Paris, and student of the Lardizabalaceae.) — DECAISNEA.

Two species, *Decaisnea insignis* with golden yellow, recurved follicles and brown seeds, of the Himalayan region, and *D. fargesii*, of China, the latter cultivated rarely in North America as a botanical curiosity.

The strange fruits of *Decaisnea*, like those of *Akebia*, have been termed follicles, this designation undoubtedly based on Hooker and Thomson's description and on Hooker's (1855, 1884) published drawings of *D. insignis* that illustrate dehisced fruits. However, no published drawings or photographs of the fruits of *D. fargesii* known to us illustrate dehisced fruits, and observations (personal communication) by Dr. J. M. Fogg, Jr., of the fruits of a plant of *D. fargesii* cultivated at the Arboretum of the Barnes Foundation have shown that they remain closed. It is on this basis that the term berry, along with follicle, is applied to the fruits of *Decaisnea* in the description above.

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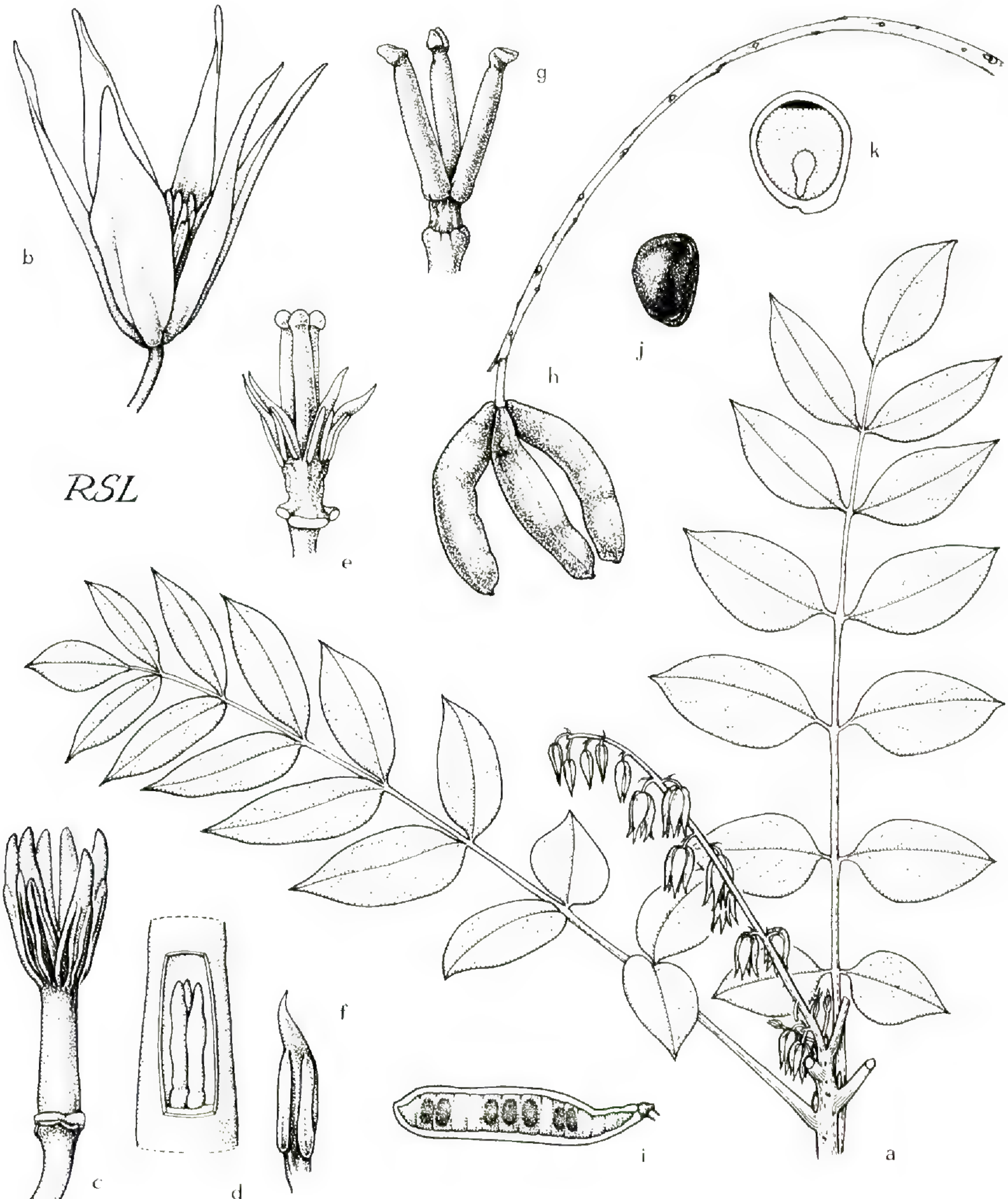

FIGURE 2. **Decaisnea.** a–k, *D. fargesii*: a, habit of flowering branch (several leaves and branches of the inflorescence removed), × 1/3; b, functionally staminate flower, × 2; c, functionally staminate flower with sepals removed, × 4; d, detail of base of staminal tube with window cut to expose rudimentary gynoecium, × 8; e, functionally perfect flower with sepals removed, × 3; f, stamen from perfect flower, × 6; g, perfect flower after anthesis showing divergent carpels, × 1 1/2; h, rachis of inflorescence and 3 mature berries (from 1 flower), × 1/3; i, mature berry with wall removed showing seeds embedded in pulp, × 1/2; j, seed, × 1 1/2; k, longitudinal section through seed showing embryo and endosperm (stippled), × 2.

1. **D. fargesii** Franchet, Jour. Bot. Morot 6: 234. 1892. FIGURE 2.

Erect shrubs to ca. 3 meters with several straight stems from the base, branching near the summit; young stems greenish tan, becoming silvery or grayish-tan, the periderm exfoliating in thin sheets; winter buds 0.6–2.4 cm. long, ± glaucous, with 2 imbricated, reddish brown, acuminate outer scales. Leaves large, 34–70(–90?) cm. long (the petiole 13–28 cm. long) with 13, 15, or 17 (or more?) leaflets, the lateral leaflets on petiolules 2–10 mm. long; leaflet blades 4.3–9.6(–15) cm. long, 1.7–5.2(–8.2) cm. wide, ovate to elliptic with attenuate to obtuse bases, entire margins, and acute to acuminate apices; upper surfaces of the blades dark green, with scattered hairs, the lower surfaces grayish green, very finely pubescent, becoming ± glabrous with age. Flowers appearing with the leaves in spring, ± pendulous on short pedicels 8–13 mm. long (each pedicel subtended by a small, acicular bract) in erect to drooping racemes and/or diffuse panicles terminating lateral branches, the rachis and pedicels becoming woody when fruit-bearing. Sepals 6, greenish yellow, inserted on the discoid receptacle, the abaxial surfaces finely puberulous, the outer whorl of 3, 17–22(–28) mm. long, to 3 mm. wide, narrowly elliptic or ± subulate, tapering to an acute apex, the inner whorl of 3 similar in length, lanceolate, 6–7 mm. wide, and strongly keeled from the purplish base. Petals absent. Androecium of functionally staminate flowers with the anther filaments connate into a tube 2.5–4 mm. long, the 6 anthers free or basally connate, 5–6 mm. long, the connectives produced into ± acute apices; stamens of functionally perfect flowers ca. 5 mm. long, the filaments connate into a short tube ca. 2 mm. long. Gynoecium of staminate flowers rudimentary, included within the staminal tube; in perfect flowers the 3 carpels inserted on a short gynophore and exserted from the staminal tube, ca. 7 mm. long at anthesis, initially erect, becoming divergent after anthesis. Fruits cylindrical blue berries 5–8(–10) cm. long, ca. 1.5 cm. in diameter, ± straight, with thick, leathery, warted walls; seeds black, oval in outline, flattened, ca. 1 cm. long, embedded in white pulp. $2n = 30$. (*D. insignis* sensu Diels, non Hooker & Thomson.)

Native to China, where herbarium records at A and GH indicate its occurrence in Anhwei, Shensi, Hupeh, Szechwan, Hunan, Kweichow, and Yunnan provinces. Despite its hardiness as far north as Boston, *Decaisnea fargesii* is rarely cultivated in North America. To insure production of the curious fruits, plants producing perfect flowers should be grown.

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A NEW HERISSANTIA (MALVACEAE) FROM THE WEST INDIES

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A RECENT COLLECTION of *Herissantia* from the Bahamas (cited below) does not conform to the description of any existing species of that genus. After first being considered new, it was subsequently discovered to agree with the description of *Abutilon trichodum*, a species described from Cuba but with a name that has been ignored in the recent literature of the family.

Sauvalle (1873) and León and Alain (1953) simply placed *Abutilon trichodum* in synonymy with *A. crispum* (L.) G. Don (= *Gayoides crispum* (L.) Small = *Herissantia crispa* (L.) Brizicky), whereas Grisebach (1864, 1866) recognized two taxa here, which he distinguished as varieties of *A. crispum*. He did so imperfectly, however, confounding *A. trichodum* with *A. imberbe* (DC.) G. Don, which is correctly a synonym of *Herissantia crispa*. The opportunity to examine the recently collected Bahamian material makes it clear that two distinct species are involved. *Herissantia crispa* is widely distributed in the Neotropics and subtropics, including the West Indies; *H. trichoda* is known at present only from Cuba and the Bahamas.

Since *Herissantia trichoda* is such a poorly known species, a complete description and an illustration (FIGURE 1) are presented here, based on *D. S. & H. B. Correll 48936* (Bahama Islands, Eleuthera, in vacant lot among brush, Tarpum Bay, 11 Aug. 1977 (A, CTES, FTG, NY)).

Herissantia trichoda (A. Richard) Fryxell, comb. nov.

Abutilon trichodum A. Richard in de la Sagra, Hist. Fis. Pol. Nat. Cuba **10**: 59. *t. 17*. 1841; Essai Fl. Cuba **1**: 155. 1841. TYPE: Cuba, *de la Sagra s.n.* (K).

Plant prostrate, the stems trailing but not rooting, terete, slender, becoming woody, 2–3 mm. in diameter near crown, minutely and evenly stellate-puberulent, the hairs ca. 0.1 mm. long, soft to the touch. Leaves gray-green; stipules inconspicuous, 0.5–2 mm. long, soft-puberulent, caducous; petiole 0.5–2 mm. long, terete, soft-puberulent like stem; blade up to 15 mm. long and 14 mm. wide (usually somewhat smaller and narrower), densely stellate-puberulent above and below, basally cordate (sometimes asymmetrically so), ovate or with a suggestion of lobes in larger leaves, crenate, acute or obtuse, palmately 5- to 7-nerved. Pedicels terete, solitary in the axils, slender (diameter ca. 0.2 mm.), up to 2 cm. long, exceeding the subtending leaves, with a prominent articulation 2–4 mm. below the flower, minutely stellate-puberulent, more sparsely so below the articulation than above; calyx minutely stellate-puberulent, cupuliform in flower, 2.5–3 mm. long, ca. half divided, the lobes ovate-acuminate, about

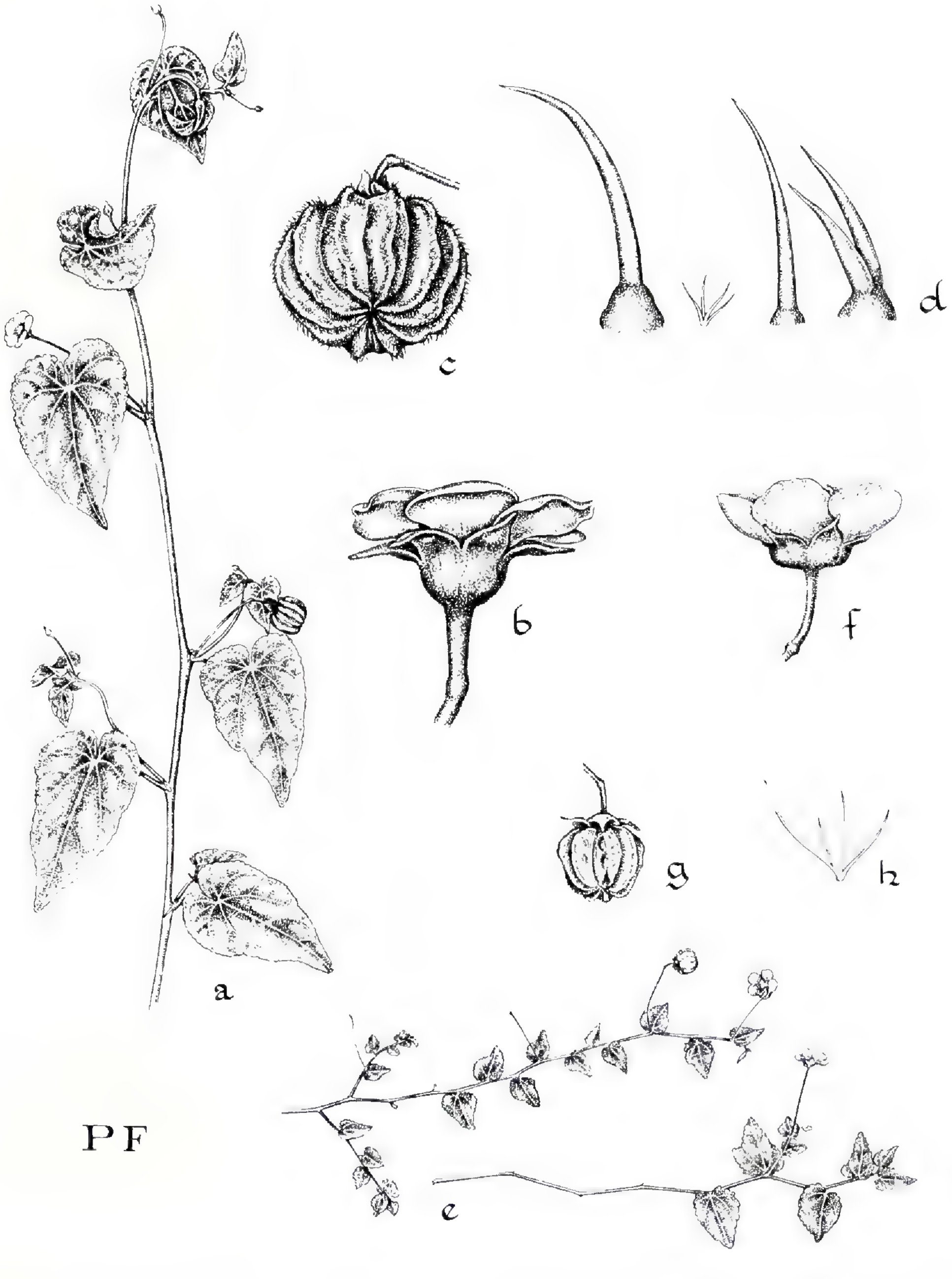

FIGURE 1. a–d, *Herissantia crispa*: a, flowering and fruiting branch, × ½; b, flower, side view, × 3; c, fruit, × 1½; d, trichomes on fruit, × 65. e–h, *Herissantia trichoda*: e, flowering and fruiting branches, × ½; f, flower, side view, × 3; g, fruit, × 1½; h, trichomes on fruit, × 65. *Drawn by Priscilla Fawcett.*

as broad as long, obscurely one-nerved, reflexed in fruit; petals white or pale yellow, ciliate on claw (cilia 0.2–0.3 mm. long) but otherwise glabrous, 4 mm. long and about as broad; staminal column ca. 1.5 mm. long, glabrous, pallid, staminiferous at apex, the stamens ca. 20, the filaments ca. 1 mm. long, the anthers golden yellow, ca. 0.5 mm. long, the pollen

yellow, spherical, echinate; styles ca. 10, exceeding the anthers, pallid, with purple capitate stigmas. Fruit oblate, more or less inflated, 7–9 mm. in diameter, 3–6 mm. high (the column 1 mm.), minutely stellate-pubescent, each mericarp 2-seeded; seeds brown, 1.2–1.3 mm. in diameter, sparingly and minutely scabridulous.

Herissantia trichoda is one of five species in the small genus *Herissantia*, in which three other species, like *H. trichoda*, have relatively restricted distributions: *H. tiubae* (K. Schumann) Brizicky is from central Brazil; *H. nemoralis* (St.-Hilaire) Brizicky from southern Brazil, northern Argentina, and Bolivia; and *H. dressleri* Fryxell from Mexico. The remaining and best-known species, *H. crispa* (Linnaeus) Brizicky, is variable (cf. TABLE 1) and is both widely distributed and common, occurring below 2000 meters elevation from the southern United States through Mexico, Central America, and the West Indies, to South America as far as Argentina and Bolivia. It is also adventive elsewhere. *Herissantia crispa* frequently occurs in disturbed ground as a weed and may well be adventive over much of its present range. *Herissantia trichoda* appears to be more closely allied to *H. crispa* than to any of the other species presently known in the genus. A detailed comparison is presented in TABLE 1.

TABLE 1. Characters distinguishing two species of Herissantia.

CHARACTER	*H. trichoda*	*H. crispa*
Leaf length (cm.)	1–1.5	up to 7
Stipule length (mm.)	0.5–2	(2–)3–8
Calyx length (mm.)	2.5–3	4–7
Calyx lobes	as broad as long	longer than broad
Petal length (mm.)	4	6–11
Staminal column height (mm.)	1.5	2–2.5
Filament length (mm.)	1	1.5–2
Fruit diameter (mm.)	7–9	13–20
Fruit height (mm.)	3–6	8–12
Column length of mature fruit (mm.)	1	1.5–2.5
Fruit vestiture	stellate-puberulent	hispid
Seed diameter (mm.)	1.2–1.3	1.5–1.7

In addition to the more easily quantified differences compared in the table, other, subtler characters also differentiate these two species. In growth habit, *Herissantia trichoda* is prostrate, whereas *H. crispa* is suberect to trailing. The other species are fully erect shrubs or subshrubs.

The leaves of *Herissantia crispa* not only are much larger but also range from long-petiolate (petioles up to 9 cm. long) on nonflowering branches to sessile on flowering ones. In *H. trichoda*, on the other hand, the leaves are always short-petiolate, with the petioles 0.5–2 mm. long.

The stems, petioles, and pedicels of *Herissantia crispa* often have long (1–2 mm.) simple hairs in addition to shorter stellate ones. Although these

long simple hairs are absent in *H. trichoda*, they are sometimes absent on *H. crispa*, so this distinction is not absolute.

The shape as well as the size of the leaves is distinctive. The leaves of *Herissantia crispa* are ovate, unlobed, acute to acuminate, and essentially symmetrical. Those of *H. trichoda* are ovate to sometimes weakly lobed, acute or obtuse, and often somewhat asymmetrical.

ACKNOWLEDGMENTS

I am grateful to Donovan Correll for bringing this interesting and unexpected plant to my attention; to Priscilla Fawcett for providing the excellent drawing; and to Antonio Krapovickas for sharing his knowledge of *Herissantia*.

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ADDENDUM

Although Richard described *Abutilon trichodum* as having four seeds per mericarp, examination of the type cited above from Cuba reveals it to have only two, in conformity with the Bahamian collection of Correll & Correll.

U. S. DEPARTMENT OF AGRICULTURE
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NOTES ON AMERICAN GRASSES

FRANK W. GOULD

THE FOLLOWING NOMENCLATORIAL NOTES have resulted from the author's systematic revisions of the grasses of the Americas.

Digitaria similis Beetle ex Gould, nom. nov.

Based on *Trichachne affinis* Swallen, Rhodora **65**: 355. 1963. TYPE: Dominican Republic. Prov. of Santiago, Quinqua, *Ekman* in 1930 (holotype, US). Non *Digitaria affinis* Opiz ex Bercht. Oekon.-tech. Fl. Böhmens **1**: 500. 1836, nec *Digitaria affinis* Roemer & Schultes, Syst. Veg. **2**: 470. 1817.

The name *Digitaria similis* Beetle (Phytologia 37: 344. 1977) is invalid because it was published without a direct reference to the page and date of publication of the replaced synonym as specified in Article 33 of the *International Code of Botanical Nomenclature*. The new name is a result of studies on the grasses of the Lesser Antilles, and will be included in the systematic treatment of the Monocotyledoneae in R. A. Howard's *Flora of the Lesser Antilles*.

Bouteloua curtipendula (Michaux) Torrey in Marcy, Expl. Red River, 300. 1853.

The citation "*Bouteloua curtipendula* Torrey in Emory, Notes Mil. Reconn. 154. 1848" reported by Griffiths (Contr. U. S. Natl. Herb. **14**: 419. 1912) and more recent authors should be corrected as indicated above.

Bouteloua hirsuta Lagasca var. **glandulosa** (Cerv.) Gould, stat. & comb. nov.

Erucaria glandulosa Cerv. Naturaleza **1**: 347. 1870. TYPE: Mexico. "Guadelupe et Moctezuma."
Bouteloua hirticulmis Scribner, U. S. D. A. Circ. **30**: 4. 1901.
Bouteloua glandulosa (Cerv.) Swallen, N. Am. Fl. **17**: 621. 1939.

The new combination in *Bouteloua* completes the series of nomenclatorial changes that the author has made in studies on the genus over a period of some 17 years. A monographic treatment of *Bouteloua* is scheduled to appear in the *Annals of the Missouri Botanical Garden*.

Aristida wrightii Nash var. **parishii** (Hitchcock) Gould, stat. & comb. nov.

Aristida parishii Hitchcock in Jepson, Fl. Calif. **1**: 101. 1912. TYPE: California. Agua Caliente, *Parish Brothers 1029a*.

The new combination in *Aristida* will appear as part of a study on the grasses of Baja California to be published by the San Diego Natural History Museum.

Department of Range Science
Texas A&M University
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A NEW COMBINATION IN BULBOSTYLIS FROM THE WEST INDIES

TETSUO KOYAMA

AS A RESULT of literature and herbarium studies of Lesser Antillean Cyperaceae, the following new combination in the genus *Bulbostylis* is made. A complete systematic treatment of the family will be published in the forthcoming volume of the *Flora of the Lesser Antilles* by Richard A. Howard.

Bulbostylis capillaris (L.) Kunth ex C. B. Clarke in Hooker f. Fl. Brit. India **6**: 652. 1893, subspecies **antillana** (Britton) T. Koyama, stat. & comb. nov.

Stenophyllus antillanus Britton, Bull. Torrey Bot. Club **43**: 447. 1916. TYPE: Dominica, *Lloyd 822*.

Bulbostylis antillana (Britton) Fernald, Rhodora **40**: 392. 1938; Kral, Sida **4**: 100. *fig. 26*. 1971.

Bulbostylis capillaris sensu C. B. Clarke in Urban, Symb. Antill. **2**(1): 88. 1900, *pro parte*, as to the Martinique specimen, non C. B. Clarke, 1893.

I regard *Bulbostylis antillana* as a subspecies of *B. capillaris*. The two species are an excellent match in details of achenes and glumes; the difference between them is based only on vegetative characters. The wiry leaves of *B. antillana* are generally twice as wide as the capillary leaves of *B. capillaris*, and are nearly smooth or only weakly scabrid in contrast to the densely hispid pubescence of the latter. Also, the culms of the former are naturally relatively more rigid than those of the latter, but without clear-cut boundaries of dimension. The inflorescences of *B. antillana* normally bear twice as many spikelets as those of *B. capillaris* and are always lax and open with several solitary spikelets only. These habital differences, however, are not always definitive because intermediate phases occur. The difference between the two, therefore, interestingly corresponds to that of the Asian *B. densa* subsp. *densa* and subsp. *trifida*.

The report of *Bulbostylis capillaris* from Martinique by C. B. Clarke was based on *Duss 758* (K, NY!, P), which was determined as *B. capillaris* var. *major*, a manuscript name given by Duss. Another specimen, *Duss 478* (*pro parte*) (NY!) from Martinique also bears a determination as *B. capillaris*. Both of these, serving as the only bases of the report of *B. capillaris* from the Lesser Antilles, are in my opinion *B. capillaris* subsp. *antillana*. The distribution of the endemic subspecies includes the Lesser Antillean islands of Dominica, Martinique, St. Lucia, and Îles des Saintes; the typical phase of *B. capillaris*, occurring in the United States, Mexico, Cuba, and the Dominican Republic, is not known from the Lesser Antilles up to now.

THE NEW YORK BOTANICAL GARDEN
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Preliminary Announcement

Thirteenth International Botanical Congress

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Journal of the Arnold Arboretum *April, 1979*

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COVER: The buds, leaves, and fruit of *Carpinus caroliniana* Walter, hornbeam or blue beech, form the basis of this year's cover design. An individual nutlet, together with its leafy, three-lobed wing, will appear on the offprints; a series of these was used in designing the device that appears on the back cover. The designs were all drawn by Karen Stoutsenberger from materials collected from plants growing in the Arnold Arboretum.

Widespread in the Northern Hemisphere, *Carpinus* L. (placed in the Betulaceae or alternatively in the Corylaceae or even the Carpinaceae), with upwards of 35 species, exhibits a disrupted Arcto-Tertiary distribution in eastern North America, Europe, Asia Minor, and in eastern Asia where the center of species diversity occurs. The only North American representative of the genus, *C. caroliniana* grows along the edges of streams and in wet, rich soils in forested areas from Nova Scotia and Quebec southward to Florida and westward into Minnesota, Iowa, Missouri, eastern Texas, and Oklahoma. Disjunct populations are known in mountainous regions of southern Mexico and in Central America.

The stems of *Carpinus caroliniana*, a small tree, have smooth, brownish- or bluish-gray, sinuate bark and an appearance reminiscent of those of beech trees (*Fagus* spp.). The wood, which is occasionally used for tool handles, is light brown to nearly white. Its growth habit, relatively small size, conspicuous infructescences, and foliage, which turns deep scarlet and orange to yellow in fall, combine to make this species an attractive native ornamental. — *S. A. S.*

Second-class postage paid at Boston, Massachusetts

This number of the Journal of the Arnold Arboretum *is dedicated to* BERNICE G. SCHUBERT, *who has recently completed her responsibilities as chairman of its Editorial Committee, a position she accepted in 1975 when the organization of the Journal staff was modified slightly. Dr. Schubert had already served as editor of the Journal for eleven years, and, despite her change of title in 1975, she continued in that capacity through the April, 1979, number of the Journal.*

During her long and close association with the Journal, Bernice Schubert maintained the high editorial standards established by her predecessors, expanded the scope of the Journal, and modernized its format and appearance. She brought to the task of editing a keen eye and a strong sense of style, as well as the botanical training and scientific knowledge necessary to carry on the Journal tradition.

The Director of the Arnold Arboretum and members of the Editorial Committee are joined by the entire staff in expressing their deep gratitude for her many, often unrecognized contributions to the Journal, the Arboretum, and the botanical community as a whole. With freedom from editorial work, Bernice is devoting her energies to her continuing taxonomic studies. We hope that she will also serve in the years to come as unofficial advisor to the Journal staff.

JOURNAL
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ARNOLD ARBORETUM

VOL. 60 JULY 1979 NUMBER 3

DICOTYLEDONOUS WOOD FROM THE UPPER CRETACEOUS OF CENTRAL CALIFORNIA

VIRGINIA M. PAGE

THE CRETACEOUS is well represented in California by extensive marine sediments, known as the Great Valley Sequence, exposed along the western border of the Central Valley. Wood occurs in limited quantities in the sequence from the Aptian through the uppermost stages. Wood also occurs in relative abundance throughout the Tertiary in all of the far western states; thus, a unique opportunity is available for the study of compositional and pattern changes encompassing a long span of time. With one exception (CASG 59858, of unconfirmed provenance [1]), the few wood specimens examined so far from Lower Cretaceous localities are gymnosperms; however, angiosperms may have been in the region by Albian time, as this sample indicates. They were certainly in the region by the Coniacian, as a specimen to be described indicates, and by Maastrichtian time angiosperms were diverse and relatively abundant, as shown not only by remains of wood but particularly by pollen (Chmura, 1973; Drugg, 1967). The present report is the first of a series summarizing the results of an investigation of a suite of fossil woods collected from the upper portions of the Great Valley Sequence. Among the samples showing sufficient anatomical structure, there are over sixty dicotyledons, fifteen gymnosperms, and one monocotyledon. Descriptions of ten dicots and one gymnosperm have been published elsewhere (Page, 1967, 1968, 1970, 1973).

GEOLOGIC OCCURRENCE AND AGE

The specimens to be described were collected from five localities. Since two of these sites are not represented in this first paper, a description of them will be presented when the specimens obtained from them are discussed. The assemblage to be described here was derived from weathered

[1] This specimen was found among the geological collections of the California Academy of Sciences. It was collected in 1929 by F. M. Anderson. According to his label, the locality is in the Chickabally Member of the Horsetown Formation. The age of this member is Aptian–Albian.

© President and Fellows of Harvard College, 1979.

mudstone at three localities in the foothills of the Diablo Range, west of the town of Patterson in Stanislaus County. The specimens occur sporadically, together with gypsum-encrusted phosphatic concretions that contain a rich assortment of pollen, spores, radiolarians, foraminifera, dinoflagellates, and other microfossils. The specific locations are as follows:

Locality 1. Del Puerto Creek; SE¼ SW¼ sect. 20, R. 7 E., T. 5 S., Oristimba 15″ quadrangle.

Locality 2a. Black Gulch; NE¼ SE¼ sect. 32, R. 7 E., T. 5 S., Oristimba 15″ quadrangle.

Locality 2b. Unnamed; NW¼ NW¼ sect. 4, R. 7 E., T. 5 S., Oristimba 15″ quadrangle.

Locality 2b lies about three-eighths of a mile south of locality 2a. The two sites lie on strike and are essentially time equivalent (J. Stein, pers. comm.). Locality 1 lies about two and one-quarter miles to the northwest of locality 2b and slightly oblique to regional strike. Chmura (1973) places locality 1 stratigraphically above locality 2a (and therefore 2b as well) and estimates the stratigraphic distance to be about 1200 feet (365 m.).

Chmura (1973), citing Bishop (1970 and pers. comm.), assigns locality 1 to the Maastrichtian on the basis of foraminiferal fauna that indicate a "C and/or D-1" zone of Goudkoff (1945). Again citing personal communication with Bishop, Chmura reports his opinion that locality 2 falls within Goudkoff's D-2 zone and is, therefore, Campanian. Most workers, however, place the boundary between the Maastrichtian and the Campanian below the D-2 zone. Acceptance of this latter interpretation would place localities 2a and 2b in the Maastrichtian. Recent work on dinoflagellate assemblages from each of the three localities has confirmed the occurrence of a typical Maastrichtian dinoflagellate assemblage in all three (J. Stein, unpubl.).

Ingersoll (1976) has described the Great Valley Sequence as a series of subsea fan deposits, and localities similar to the above as probably basinal facies. Since this mode of deposition has great bearing on assessments of the ecological and evolutionary significance of the suite of fossils to be described, it will be discussed more fully later.

SYSTEMATICS

Fossil woods have long been the despair of paleobotanists because of the many problems associated with attempts to find modern correlatives. Despite the seemingly insurmountable obstacles, these fossils remain an excellent source of information about past vegetation. The stem is an important part of the plant. It is reasonable to suppose that this has always been so; therefore, the evolutionary history of the stem is as essential as that of any other part of the plant in our search for answers to the question of the origin of the angiosperms and their subsequent diversification.

Moreover, although evolutionary pathways can be inferred from the study of modern woods, as I. W. Bailey and his students have shown, the rate and extent of specialization in the past can be known only from the fossil record. The kinds of facts needed for this aspect of paleobotany can (and should) be obtained independently of reference to presumed relationships of fossils to modern taxa.

The factors that contribute to frustration in dealing with fossil woods are numerous and stem chiefly from three sources: state of preservation, serious gaps in our knowledge of modern woods, and age of the fossils. Fossils are organisms or parts of organisms that have, for the time being, partially or completely escaped the recycling process that is a fundamental part of nature. The state of preservation of such relics varies according to the amount and kind of degradation that preceded mineralization, to the degree of distortion due to the pressure of the overlying rock burden, and to other post-depositional physical and chemical processes. Of the characters most likely to be preserved in secondary xylem, the most important are: distribution of the various cellular components, size of the vessel elements, type of perforation plate, type of intervessel pitting, ray structure, fiber structure, and presence and distribution of tracheids, included phloem, oil cells, resin or gum ducts, and crystals. Unfortunately, circumstances leading to the final condition of preservation too often obscure or obliterate some essential features. Although the presence of a particular feature can be demonstrated, the fact of primal absence can not always be assumed if it can not be observed. For example, in specimens with scalariform end plates averaging less than 20 bars, there are times when it is not possible to be certain that all plates were scalariform, particularly if the vessels are filled with tyloses. Distortion of the grain due to pressure often obscures or alters the appearance of rays, the presence of growth rings, and the distribution of parenchyma and vessels. Degradation by microorganisms may destroy essential components of either the primary or the secondary wall of cells. In some cases nothing remains of the cells but the middle lamella or the primary walls, while in others the primary walls have largely disappeared, leaving only secondary walls. Needless to say, such structures as wall pitting and bars of perforation plates, not to mention spiral thickening and fiber septae, may be greatly altered by the disintegration of either the primary or the secondary wall. Provided that a sufficient amount of wall material of any kind remains, the presence or absence of wall pits or perforation plate bars is not affected; the effect is on the border in the case of pits, and on the thickness of bars in the case of perforation plates. Important features such as the arrangement of pits and the number of bars in the end plates may still be preserved.

Even when we are fortunate enough to have well-preserved specimens, we are faced with important gaps in our knowledge of modern woods. One of the more serious problems encountered in evaluating the assemblage to be described is that 70 percent of the specimens are small branches or roots, less than five centimeters in diameter. It is well known

that in woody dicots the early increments of secondary xylem are often structurally different from those in later-formed wood (Bailey & Tupper, 1918), and that the duration of the early or immature stage varies among genera (Bailey, 1924). Because of the changes that take place before structural features become established, most descriptive studies are based on mature woods. Very little, therefore, is known about the duration and kinds of changes that occur during maturation of the stem or root of any one genus. These gaps in our knowledge present serious obstacles in the way of efforts to find modern counterparts of fossilized branch or root material unless distinctive structures are present in the fossils. The presence of pith or bark is of little assistance because our knowledge of these tissues is totally inadequate for the purpose of comparative studies.

Other variables that must be considered and about which information is limited are those arising from differences that may exist in mature secondary xylem from different parts of the plant, for example, reaction wood or crotch wood (summarized in Carlquist, 1961). Unless the primary xylem is present, there is no way of knowing whether a sample of petrified wood is from a root or a stem. Such characters as pore distribution, ray structure, growth rings, and amount and distribution of parenchyma may differ widely between root and stem of the same plant. Similarly, the length of vessel elements and fibers, as well as the structure of rays, may vary considerably from the normal in and around the fork of a branching system. Ecological factors often affect the diameter and frequency of vessels as well as the presence or absence of spiral thickening among related species or among individuals of the same species (summarized in Carlquist, 1975). These kinds of variation are seldom included in descriptions of wood. Finally, because most research on wood has been performed for the purpose of identifying or determining the properties of commercially important timbers, information about the large number of noncommercial woods is limited. Although there has been a renewed interest in comparative anatomy in recent years, relatively few families have been analyzed in detail, so such important information as the ranges of variation within and among families is scanty. Because of circumstances of availability, size of the wood specimen, and the amount actually examined, it can seldom be said that the fossil material examined in detail by an investigator represents an adequate sampling of the species from which a particular specimen was derived. Since variation occurs not only within a species today but also within a given individual, it is unwise to assume that these fossils are typical of the species they now represent.

Can we assume that the species or genus or family even exists today? If the concept of organic evolution has any validity in fact, one would expect many changes to have taken place among the dicots since the close of the Cretaceous period. That changes have occurred is indicated by the experience of many paleobotanists working with plant organs from the early Tertiary or older strata. A particularly illustrative case is that of the Eocene London Clay flora (Reid & Chandler, 1933). Although the fossil

assemblage consists of a variety of plant parts, the important constituents and the ones that have been thoroughly investigated are fruits and seeds; thus, it would present a better picture of the relationship with modern taxa as they are circumscribed than would assemblages of wood or leaves. The authors found that two-thirds of the genera they recognized cannot be aligned with modern genera. Moreover, in a perusal of Chandler's summary (1964), I observed that about 15 percent of the angiosperms listed for the early Eocene of southern England could not be placed in a modern family, and about 47 percent could be accommodated in families but not in extant genera. The remaining 32 percent closely resembled fruits and seeds of modern genera but were unlike any modern species. It is not unreasonable to assume that the percentage of extinct genera would be greater among Late Cretaceous fossil assemblages.

Recently, the attention of plant anatomists (see Braun, 1970; Baas, 1973; Carlquist, 1975) has been focused on the relationship between physiological requirements of the plant and structure of its wood. Carlquist (1975) suggests that not only is there a close correlation between structure and habitat, but that evolutionary changes in angiosperms as a whole have been affected by responses to changes in the environment. In light of this idea, similarities I have observed in woods of certain species in such families as the Lauraceae, Leguminosae, Combretaceae, Moraceae, and Anacardiaceae may be attributed to similarity in responses to ecological factors. The basic pattern common to these families (simple perforation plates, alternate intervessel pits, slightly heterogeneous rays, paratracheal parenchyma, septate fibers) is modified in similar directions. In all the groupings the tendency is toward amplification of axial parenchyma, and toward storeying of elements. One can ask whether these similarities reflect genetic relationship or merely a similarity in adaptive responses. That genetic affinities probably do not account for the similarities is indicated by phylogenetic schemes based on reproductive structures primarily (Cronquist, 1968) and on leaves (Hickey & Wolfe, 1975). In both systems, not only is each family mentioned above placed in a different order, but at least three subclasses are represented (Hickey and Wolfe differ from Cronquist in the placement of the Myrtales, although all three authors agree that the family Combretaceae belongs to this order). The basic pattern described above may be considered a common type of alteration from the unspecialized multiperforate condition and regarded as a stage in an evolutionary sequence. Such a sequence from a generalized multiperforate condition to simple perforations with concomitant qualitative and quantitative changes in other cellular components can be observed not only in many orders of dicots but also within families — for example, the Icacinaceae, Dilleniaceae, Araliaceae, and Cunoniaceae.

Because many plant groups have responded to environmental conditions in similar ways (one result of which is closely similar wood patterns), and there is no reason to believe that this phenomenon is of recent origin, it is my opinion that one should be wary of relying on similarity alone as a criterion for judging whether a fragment of fossil wood represents a par-

ticular modern taxon. Although I advocate great caution in identifying Cretaceous woods with modern forms, I am fully aware that in dealing with any one specimen there may be a 40 percent chance that it belongs to a modern genus; however, there is also a 60 percent chance that it does not. It is essential, therefore, that we look at the fossil record unbiased by schemes of classification based on floral parts alone. One wishes to know how far back in time modern taxa can be traced, but incautious assumptions may only serve to obscure their evolutionary history.

In view of the prevalence of parallel evolution in wood patterns and the possibility that most modern genera and many families were not in existence in the Upper Cretaceous, it seems clear that taxonomic circumscriptions of extant groupings at the genus or family level should not be applied to dispersed Cretaceous plant fragments. Because of the formidable obstacles outlined above, it is particularly important to consider an alternative procedure for evaluating the relationship between Cretaceous and modern woods. The procedure adopted here is such an alternative and consists simply of a reclassification of modern woods solely on the basis of anatomical characteristics. The result is an artificial system that does not necessarily coincide with distinctions based on floral parts. Generalized patterns, such as those observed in the majority of specimens in the Cretaceous assemblage to be described, reflect a continuum of variation within and among taxa. This continuum is reticular rather than linear. Overlapping and convergence of ranges of variation are common, often among unrelated genera. There are a few basic combinations of primitive, relatively primitive, or otherwise unspecialized wood patterns shared by a large number of genera of varying degrees of relationship.

Because information about wood patterns in many modern genera is lacking or unavailable, it is not possible at the present time to construct a classification complete enough to permit recognition of lower-order-form taxa; therefore, I prefer not to give formal recognition to the groupings of fossils described here. For the present, reference to an individual specimen will be by its accession number. To provide a temporary frame of reference, modern woods (570 genera representing 158 families) were classified on the basis of the information available to me. The characters used in this classification are those most likely to be included in descriptions or to be preserved in fossils. The major groupings and their characteristics are presented below in the form of a synoptical key.

A Classification of the Secondary Xylem of Dicotyledons

Vessels absent. ..... Group I.
Vessels present.
  Perforation plates scalariform.
    Pores mostly solitary.
      Bars in perforation plates average more than 50. ..... Group II.

Parenchyma sparse or absent. ..... IIA.
Parenchyma apotracheal only. ..... IIB.
Parenchyma paratracheal present. ..... IIC.
Bars in perforation plates average fewer than 50. ..... Group III.
Parenchyma sparse or absent. ..... IIIA.
Intervessel pits scalariform. ..... IIIA sect. 1.
Intervessel pits transitional/opposite. ..... IIIA sect. 2.
Intervessel pits opposite-alternate. ..... IIIA sect. 3.
Intervessel pits alternate. ..... IIIA sect. 4.
Parenchyma mostly apotracheal. ..... IIIB.
Intervessel pits scalariform. ..... IIIB sect. 1.
Intervessel pits transitional/opposite. ..... IIIB sect. 2.
Intervessel pits opposite-alternate. ..... IIIB sect. 3.
Intervessel pits alternate. ..... IIIB sect. 4.
Paratracheal parenchyma present. ..... IIIC.
Intervessel pits scalariform. ..... IIIC sect. 1.
Intervessel pits transitional/opposite. ..... IIIC sect. 2.
Intervessel pits opposite-alternate. ..... IIIC sect. 3.
Intervessel pits alternate. ..... IIIC sect. 4.
Pores in multiples as well as solitary.
Bars in perforation plates average more than 50. ..... Group IV.
Parenchyma sparse or absent. ..... IVA.
Parenchyma apotracheal only. ..... IVB.
Paratracheal parenchyma present. ..... IVC.
Bars in perforation plates average fewer than 50. ..... Group V.
Parenchyma sparse or absent. ..... VA.
Parenchyma apotracheal only. ..... VB.
Paratracheal parenchyma present. ..... VC.
Perforation plates simple and scalariform.
Pores mostly solitary. ..... Group VI.
Parenchyma sparse or absent. ..... VIA.
Parenchyma apotracheal only. ..... VIB.
Paratracheal parenchyma present. ..... VIC.
Pores in multiples as well as solitary. ..... Group VII.
Parenchyma sparse or absent. ..... VIIA.
Parenchyma apotracheal only. ..... VIIB.
Paratracheal parenchyma present. ..... VIIC.
Perforation plates simple.
Intervessel pits scalariform, transitional, or opposite. ..... Group VIII.
Parenchyma sparse or absent. ..... VIIIA.
Parenchyma apotracheal only. ..... VIIIB.
Paratracheal parenchyma present. ..... VIIIC.
Intervessel pits alternate.
Parenchyma sparse or absent. ..... Group IX.
Parenchyma more or less abundant.
Parenchyma apotracheal only. ..... Group X.
Parenchyma diffuse. ..... XA.
Parenchyma banded or terminal. ..... XB.
Paratracheal parenchyma present. ..... Group XI.
Parenchyma vasicentric. ..... XIA.
Parenchyma aliform and/or confluent. ..... XIB.

SYSTEMATIC DESCRIPTIONS

Microscopic details of the fossils were obtained from thin sections. In the descriptions to follow, the omission of a feature of diagnostic importance means that it was not possible to observe that feature. In many specimens it was not possible to obtain a statistically significant reading of the number of vessels in a square millimeter because of distortion of the tissues; therefore, this feature has not been included. In a general way the relative frequency of pores can be inferred from the illustrations. The length of vessel elements was calculated by measuring the distance between outer limits of perforation plates except in instances where the end walls were clearly visible. An effort was made to obtain at least ten measurements of pore size and vessel element length for each specimen. The term "pore" is used in reference to the vessel as it appears in transverse section. The term "fiber" is used in its generic sense as defined in the *Multilingual Glossary of Terms Used in Wood Anatomy* (1964).

All thin sections are deposited in the Geological Collections of the California Academy of Sciences in San Francisco (CASG).

The specimens to be described in the first paper are classified in groups I, II, and III.

Group I is represented by two specimens, both of which were collected from locality 1. *Tetracentronites panochensis* has been described elsewhere (Page, 1968). Vesselless secondary xylem occurs in ten modern genera and five families.

CASG 60116

FIGURES 1, 2, 4.

MATERIAL. Small twig about 7 mm. in diameter. Growth rings not apparent.

Secondary xylem. Vessels lacking. Tracheids small, thick walled, average diameter 26 μm. (13–38). Pits small, round; pits to ray cells somewhat larger. Parenchyma abundant. Rays uniseriate and multiseriate, the latter 4 or 5 cells wide, the cells square or upright, thick walled, with minute pits on tangential walls. Multiseriates originate at pith. Uniseriates numerous, the cells high, upright.

Pith. Appears to be homogeneous; cells large.

Phloem. Multiseriate rays flare out slightly. Outer phloem or cortex with a more or less continuous ring of a variety of sclereids.

FIGURES 1–10. 1, 2, 4, CASG 60116: 1, transverse section, × 70; 2, radial section, × 47; 4, transverse section showing phloem, × 47. 3, 5–7, CASG 60117: 3, transverse section, × 4; 5, radial section showing square cells of ray, × 70; 6, transverse section, × 70; 7, tangential section showing uniseriate rays and portion of large ray, × 70. 8–10, CASG 60119: 8, transverse section, × 80; 9, radial section (note ray pits), × 80; 10, tangential section, × 80.

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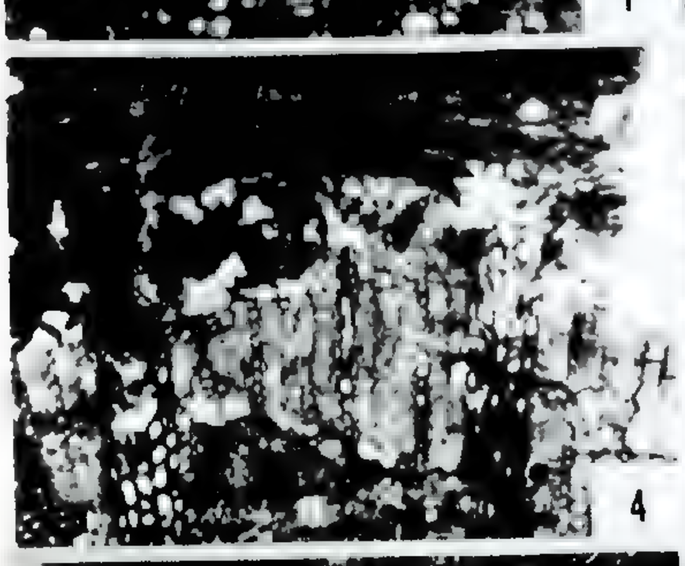
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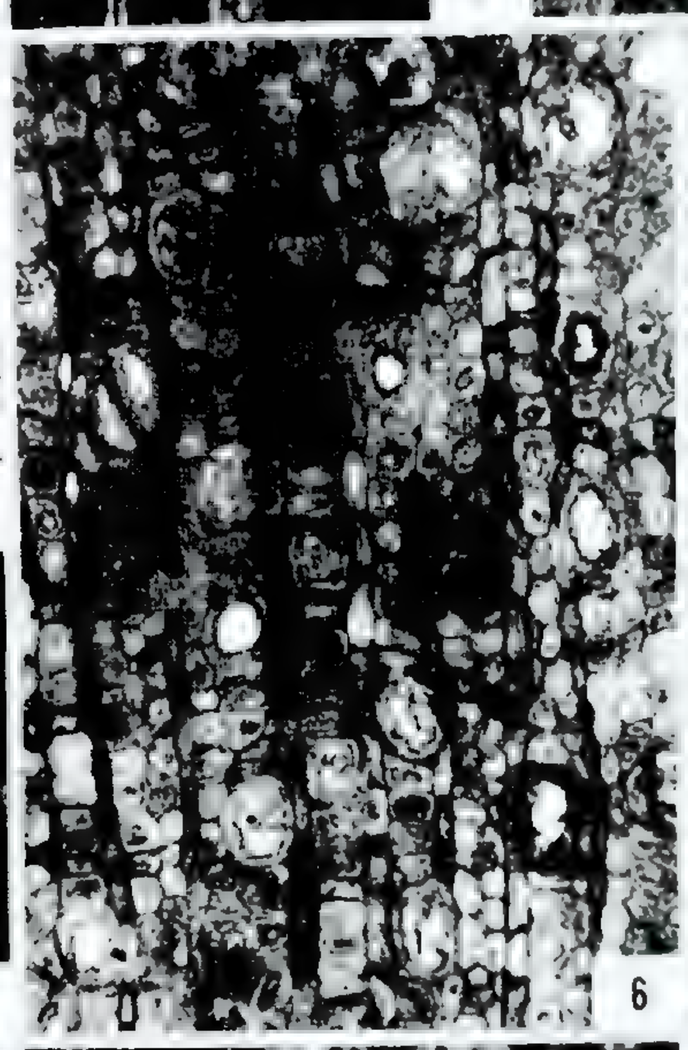
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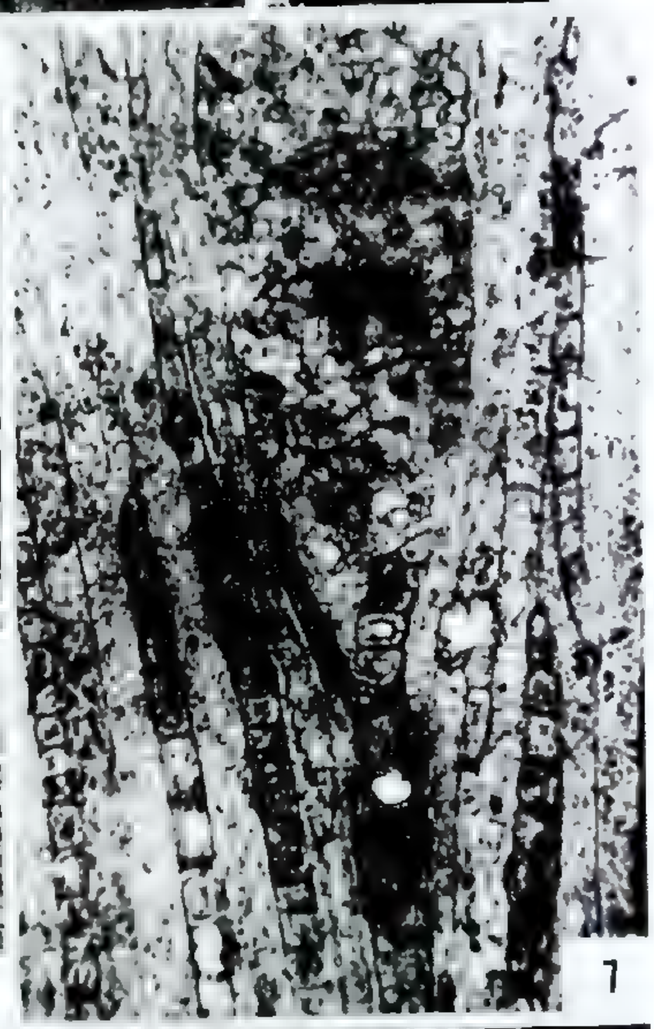
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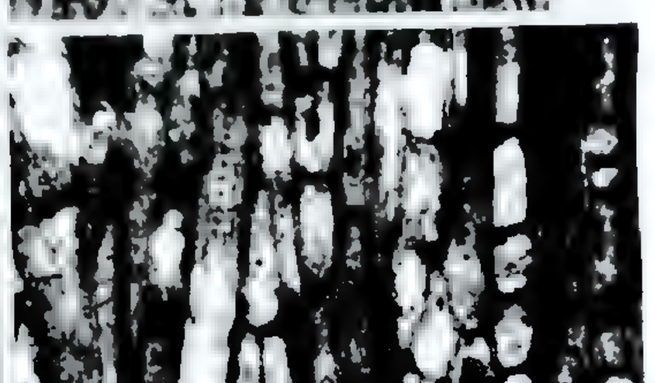
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LOCALITY. Del Puerto Creek, locality 1.

A true tangential section was not obtained. As far as can be determined, the general structure is most like that of Old World Winteraceae. New World species, as well as *Tetracentron, Amborella*, and *Sarcandra*, have little or no parenchyma. This fossil differs from *Tetracentronites panochensis* Page in its narrower rays, abundant parenchyma, and round pits. Because of poor preservation, pitting can be observed in only a few tracheids. Some modern species of Winteraceae produce small, round pits in narrow tracheids and scalariform pits in wide tracheids, while others produce only round pits regardless of the diameter of the cell (Carlquist, 1975). It is possible that later-formed tracheids (if the stem produced additional xylem increments) may have borne scalariform pits. *Trochodendron* has some axial parenchyma, but in mature wood the cells of the multiseriate portion of rays are procumbent and tracheids in early wood have scalariform pits. Information about young stems was not available.

The next five specimens are classified in Group II. The first, CASG 60120, falls in IIA and has septate fibers and vessel elements averaging less than 1 mm. in length. A similar pattern can be observed in the genus *Illicium* (Illiciaceae) and in *Matthaea* (Monimiaceae). The next four specimens (CASG 60117, CASG 60118, CASG 60119, and CASG 60130) fall in IIB. All have vessel elements over 1 mm. in length. Modern woods that are classified as Group IIB and that have this characteristic occur in such families as the Cornaceae, Theaceae, Dilleniaceae, Nyssaceae, Icacinaceae, Aquifoliaceae, Symplocaceae, and Clethraceae.

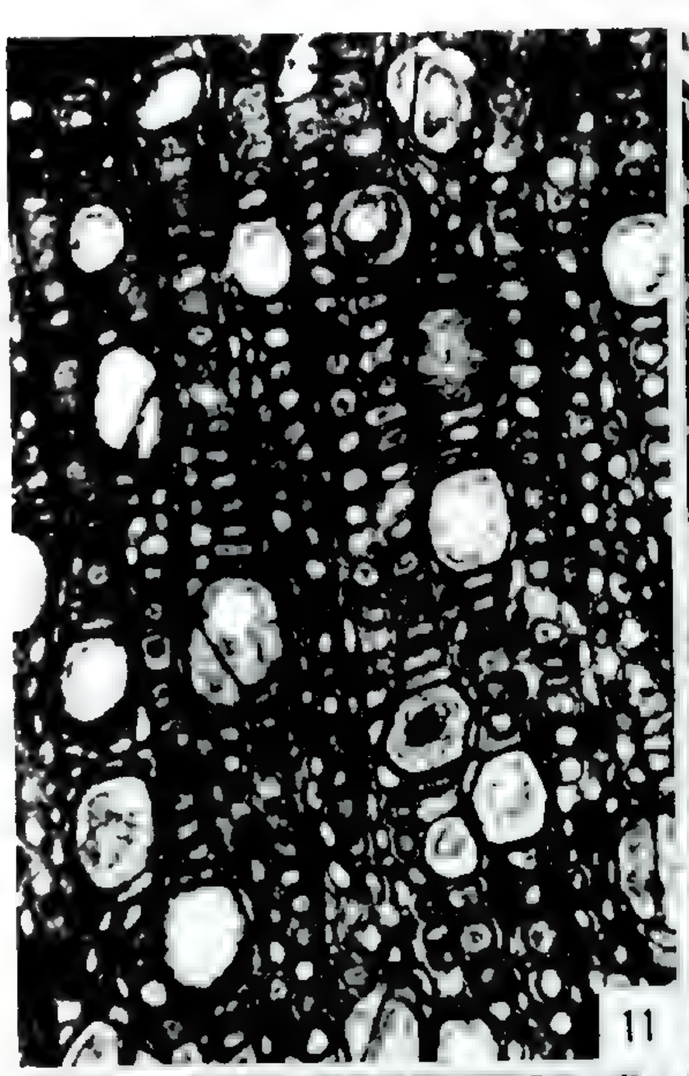
CASG 60120

FIGURES 17–20.

MATERIAL. Stem 3 cm. in diameter. Some primary xylem present.

Secondary xylem. Growth rings indistinct. Pores small, scarcely larger than fibers in transverse section, squarish, average radial diameter 33 μm. (29–39), average tangential diameter 32 μm. (26–37). Perforation plates scalariform, bars average 58 (20 to 70). Intervessel pits scalariform-transitional, grading into alternate in some; pits to ray cells similar, some small, round, and alternate; length of vessel elements about 600–800 μm. Parenchyma seems to be absent. Rays heterocellular, 2 to 4 cells wide, highly disorganized, cells in center of ray square or short procumbent, uniseriate margins one cell high, the cells upright; uniseriates up to 9 cells

FIGURES 11–20. 11–13, CASG 60118: 11, transverse section, × 75; 12, radial section, × 40; 13, tangential section (note high multiseriate ray), × 50. 14–16, CASG 60122: 14, transverse section, × 43; 15, radial section, × 70; 16, tangential section, × 75. 17–20, CASG 60120: 17, transverse section, × 73; 18, tangential section, × 60; 19, radial section (note high upright cells of uniseriate rays), × 40; 20, radial section showing square and upright cells of multiseriate ray (note fiber septae in upper right), × 40.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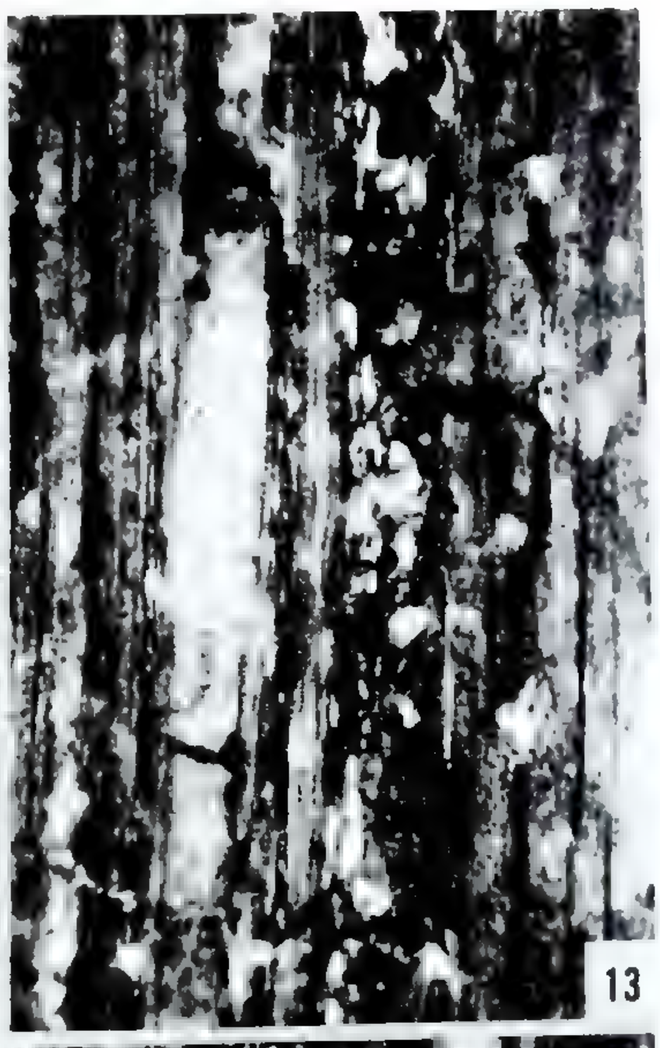
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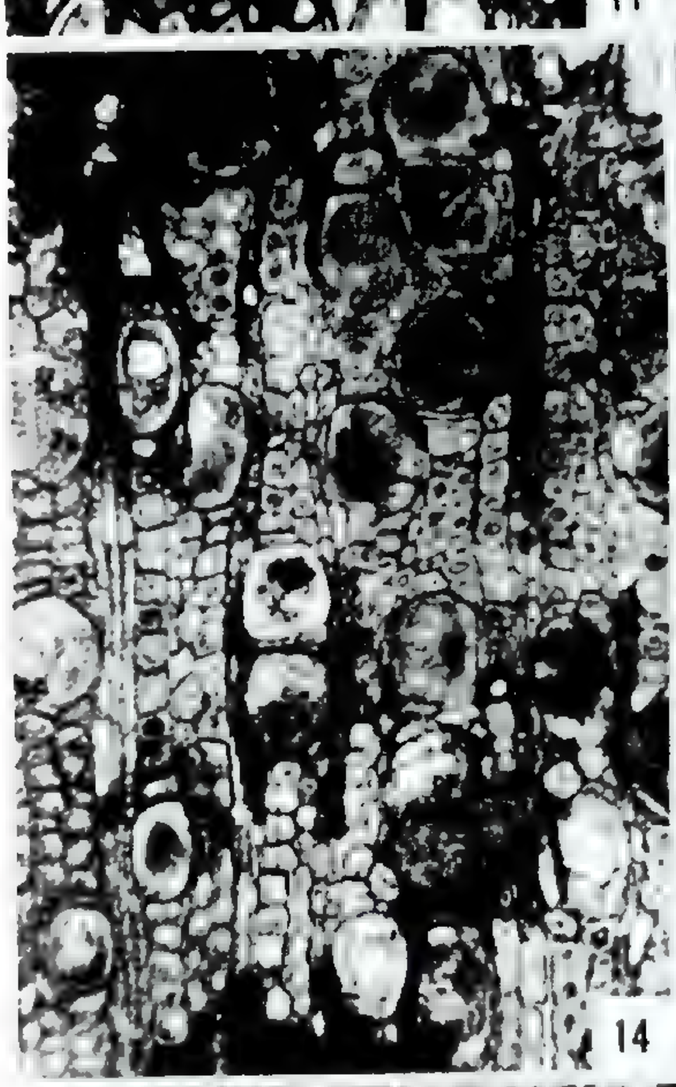
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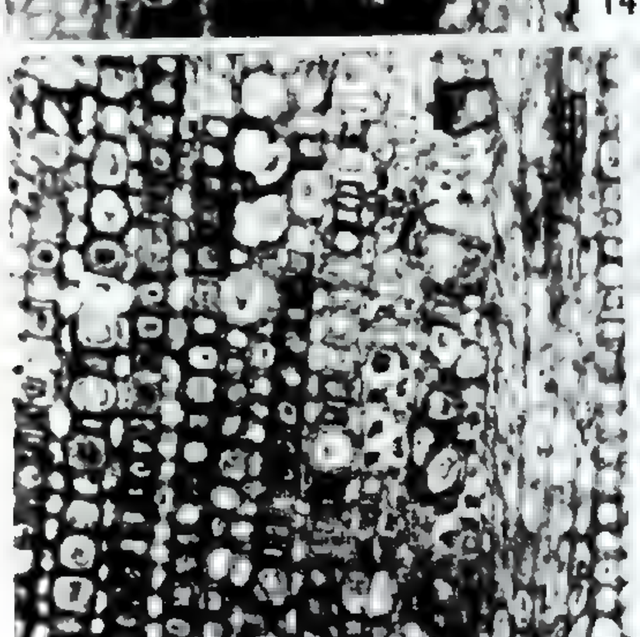
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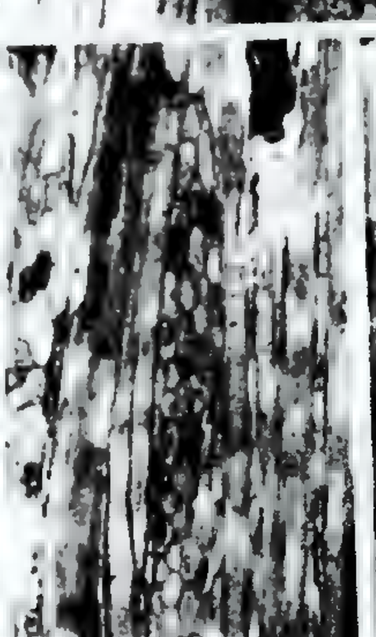
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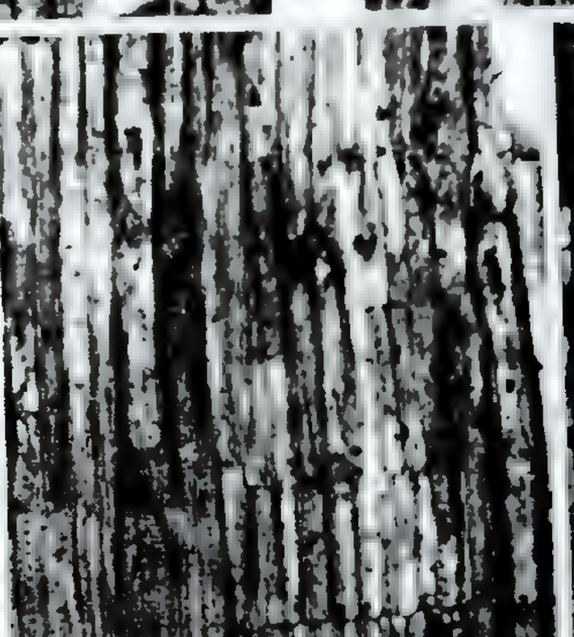
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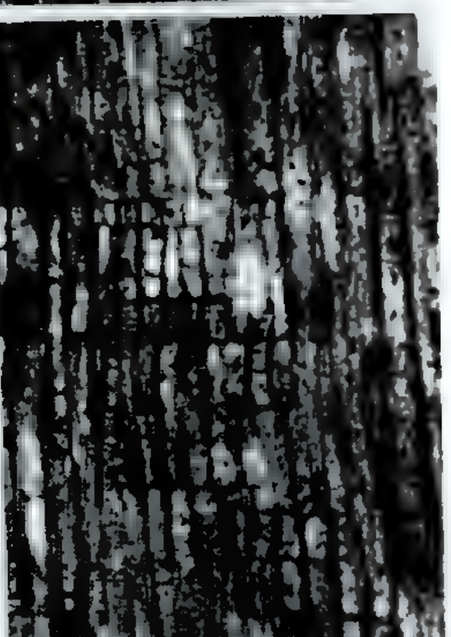
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high, the cells high, upright; most ray cells contain a dark, amorphous substance. Many fibers septate.

LOCALITY. Unnamed site, locality 2b.

Cells of the uniseriate rays and of the uniseriate margins of the multiseriate rays are so high that they are difficult to distinguish from parenchyma cells. The absence of parenchyma is, therefore, not certain. Septate fibers, however, usually do not occur in wood with much apotracheal parenchyma. Perforation plates are at such an acute angle and are so long that it is possible to mistake bars of the plates for intervessel pits. The general pattern is similar to that of some species of *Illicium*, but, although septate fibers have been reported in one species by Kanehira (1921), they have not been observed in the species examined by me or by Metcalfe and Chalk (1950). There is a similarity to the wood of *Matthaea* of the Monimiaceae. Septate fibers are present in this genus, but the rays are very high. Vessel elements in the fossil are much shorter than those reported for mature wood of either *Illicium* or *Matthaea*. The length of these elements in immature wood is not known to me. Pollen similar to that of *Illicium* has been reported from locality 1 (Chmura, 1973).

CASG 60117 FIGURES 3, 5–7.

MATERIAL. Small stem 3 cm. in diameter. Growth rings visible with magnification; diffuse porous.

Secondary xylem. Pores solitary, small, more or less square, average radial diameter 58 μm. (35–70), average tangential diameter 52 μm. (29–57). Perforation plates scalariform, 50 to 100 closely spaced bars. Intervessel pits scarce, some appear to be scalariform; pits to ray cells small, opposite, some elongated horizontally; average length of vessel elements 1287 μm. (870–1824). Parenchyma diffuse, moderately abundant, some cells associated with vessels. Rays uniseriate, 40 to 60 cells high, cells mostly square and short procumbent.

Pith. Small; cells small, cuboidal.

Phloem. Rays uniseriate, not as frequent as in xylem. Cells become laterally extended in outer portion, walls become thickened. Groups of stone cells in outer layers. Fibers thick walled.

LOCALITY. Del Puerto Creek, locality 1.

The size and shape of the pith varies among different sections from more or less lobed to round. The former probably represents a nodal region, the latter an internode. The departure of portions of several branch traces can be observed in longitudinal section. The nature of the departure from the pith indicates an alternate branching system. High multiseriate rays occur in restricted areas in some tangential sections (FIGURE 7). These are probably branch traces. A radial section through the pith shows two

traces departing within a very short distance (2 mm.) of one another. In tangential section the traces are confined to a narrow portion. I assume that this represents a type of phyllotaxy in which the leaves are in close approximation vertically but not necessarily radially. Of the plants I have examined, those with crowded branches have small leaves.

Poor preservation obscured wall pits in most cells. It is not uncommon for solitary vessels to be devoid of pits except where the walls are in contact with parenchyma or where ends of elements in vertical file overlap. In several areas pits in the walls of ray cells are clearly visible, but in others it is difficult to determine whether the pits are on the ray cells or on walls of vessels. In addition, the excessively long perforation plates can be mistaken for scalariform wall pits where only a portion can be seen in radial section. Some vessels contain an amber-colored substance. There is some evidence of crystals in the phloem. Occasional parenchyma cells appear to have divided transversely, resulting in a vertical series of four small cells, each of which contains a small druse. Such crystals were not observed in other cell types.

The general features of the secondary xylem, to the extent that they can be observed, occur in *Clethra*, *Nyssa*, and certain genera of the Theaceae.

CASG 60118 FIGURES 11–13.

MATERIAL. Small stem 2.5 cm. in diameter. No growth rings apparent.

Secondary xylem. Pores solitary with some tendency to form multiples, overlapping pairs tangential, average radial diameter 68 μm. (46–87), average tangential diameter 59 μm. (40–80). Perforation plates scalariform, 50 to 100 fine bars, anastomoses frequent. Vessel pits scalariform-transitional; pits to ray cells and axial parenchyma similar; vessel elements average 1108 μm. (870–1334) in length; tyloses frequent. Parenchyma diffuse, not abundant. Rays high, multiseriates 4 to 8 cells wide, cells square and upright; uniseriates numerous, very high, cells upright. Fiber pits bordered, numerous in uniseriate vertical files, apertures included.

Pith. Round; numerous primary xylem points flanked by multiseriate rays; cells small, round, vertically elongated.

Phloem. Multiseriate rays of xylem continue into secondary phloem where they flare out as a result of lateral expansion of cells. Uniseriates also extend into phloem and together with thin-walled cells and fibers form wedges alternating with inverted wedges of expanded multiseriate rays. Each wedge of conducting cells and uniseriate rays capped by a small group of fibers.

LOCALITY. Black Gulch, locality 2a.

Similar wood patterns can be found in such families as the Nyssaceae, Theaceae, Icacinaceae (*Platea*), and Aquifoliaceae (*Phelline*).

CASG 60119 FIGURES 8–10.

MATERIAL. Small stem 3.5 cm. in diameter. Growth rings faint.

Secondary xylem. Pores mostly solitary with some tangentially aligned in clusters of 2 to 4, angular, average radial diameter 104 μm. (81–110), average tangential diameter 80 μm. (69–92). Perforation plates scalariform, bars average 53 (47 to 65), some reticulate. Intervessel pits small, transitional-opposite; pits to ray cells similar; vessel elements average 1156 μm. (980–1276) in length; tyloses thin walled. Parenchyma abundant, diffuse. Rays numerous, each vessel flanked by a ray of some kind; multiseriates high, some vertically joined and some dissected, mostly 4 to 5 cells wide, the cells square, upright, and short procumbent, sheath cells common; uniseriate margins up to 14 cells high, cells upright; uniseriates up to 14 cells high, cells square and upright. Fiber pits numerous, small, bordered, on all walls, apertures included.

Pith. Round; primary xylem points numerous; cells large, flattened in long section, arranged in vertical rows.

LOCALITY. Black Gulch, locality 2a.

Group IIB woods with vessel elements over 1 mm. in length and small intervessel and vessel–ray pits are: Nyssaceae, Clethraceae, and some Theaceae.

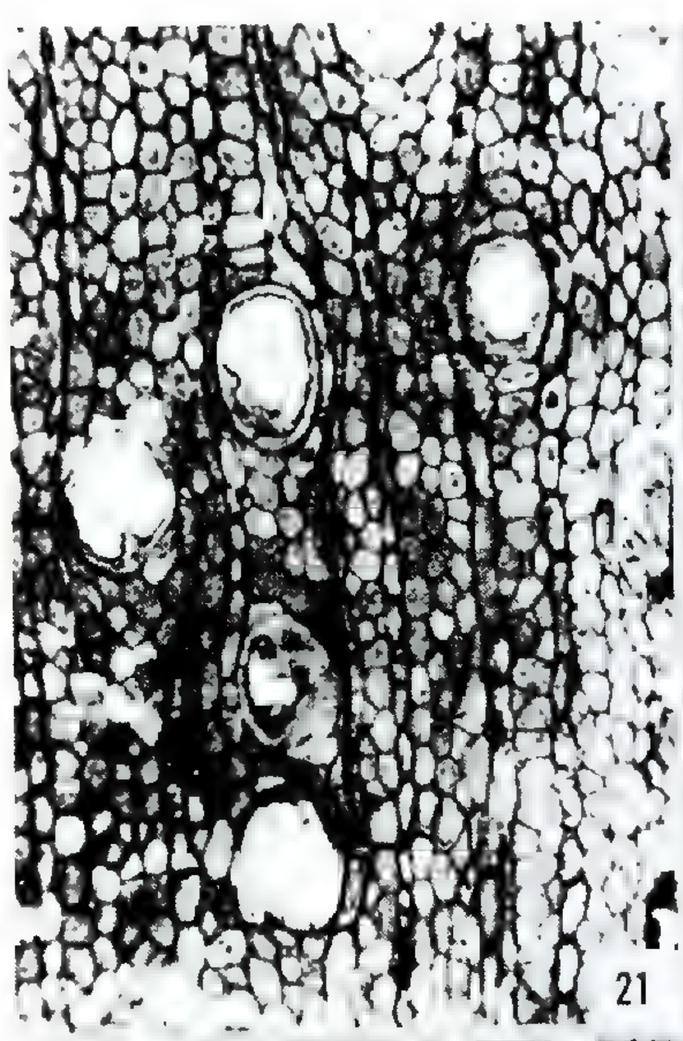
CASG 60130 FIGURES 24–27.

MATERIAL. Portion of a small branch 1.5 cm. from the pith through the phloem, which is 2 mm. thick at its widest.

Secondary xylem. Pores solitary, small, squarish, average radial diameter 46 μm. (40–58), average tangential diameter 45 μm. (40–52). Perforation plates scalariform, average 54 (25 to 99) closely spaced bars. Intervessel pits opposite-transitional, scalariform and bordered in ligules of some, occasionally on entire wall; pits to rays similar; pits to parenchyma scalariform; average vessel element length 1008 μm. (782–1132). Parenchyma abundant, diffuse, some in tangential uniseriate rows, many cells high, contents brown. Rays up to 12 cells wide, 5–7 mm. high, cells square and upright, uniseriate margins lacking; uniseriates of narrow, upright cells in tangential view, numerous, up to 12 cells high; multiseriates frequent, more or less equidistant, narrow at pith becoming wider in later increments, some dissected. Fibers thick walled, the pits small, bordered, on all walls.

Pith. Small; cells small at periphery and larger at center, rectangular in long section. Medullary rays separate protoxylem points.

Phloem. All rays continue into phloem; broad rays dip into xylem at cambium junction and flare out slightly in outer layers of phloem; walls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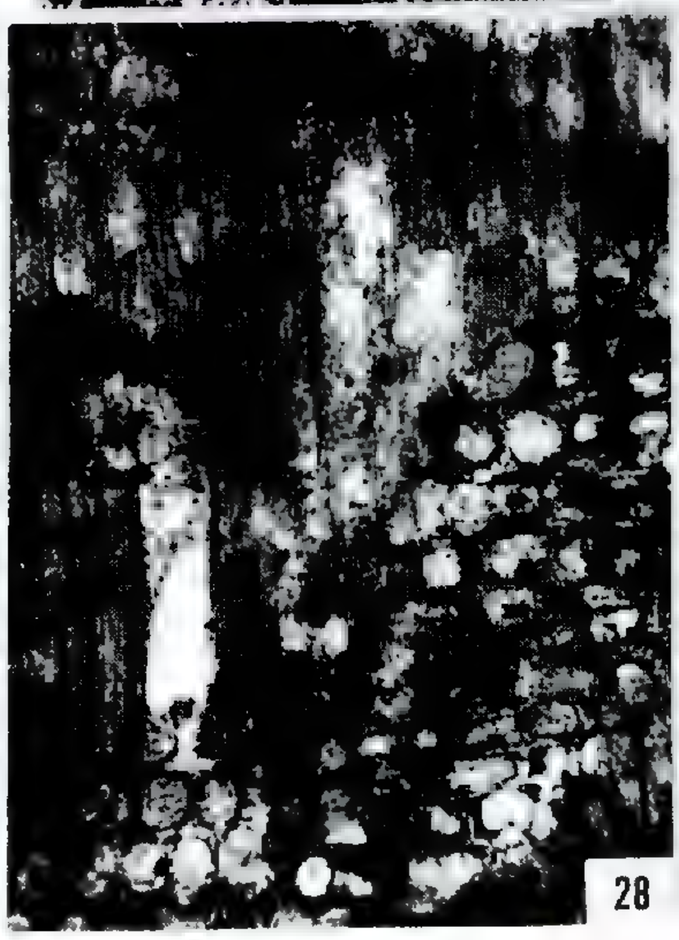
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FIGURES 21–29. 21–23, CASG 60129: 21, transverse section, × 60; 22, radial section, × 60; 23, tangential section, × 40. 24–27, CASG 60130: 24, transverse section, × 65; 25, transverse section showing phloem (note regular spacing of multiseriate rays), × 30; 26, radial section, × 65; 27, tangential section, × 65. 28, 29, CASG 60131: 28, radial section, × 60; 29, tangential section, × 60.

of fibers thick, lumen almost obliterated in some; rhomboidal crystals in some parenchyma cells.

LOCALITY. Black Gulch, locality 2a.

Except for the subfamily Dillenioideae of the Dilleniaceae, Group II woods with similar patterns have vessel elements shorter than 900 μm. (Cyrillaceae, Icacinaceae, Eupteleaceae).

The following 11 specimens (CASG 60122, CASG 60127, CASG 60208, CASG 60124, CASG 60126, CASG 60125, CASG 60128, CASG 60129, CASG 60131, CASG 60132, and CASG 60134) are classified in Group IIIB section 2. Some extant genera in this group with vessel elements longer than 900 μm. are members of the Dilleniaceae, Theaceae, Symplocaceae, Nyssaceae, Euphorbiaceae (*Protomegabaria*), Daphniphyllaceae, Buxaceae, and Cornaceae. Genera of this category with vessel elements shorter than 900 μm. belong to the Theaceae, Cunoniaceae, Cornaceae, Icacinaceae, Buxaceae, Ericaceae, Escalloniaceae, and Hamamelidaceae.

The first seven specimens are closely similar but differ in a few details. While some of these differences are the kinds that can be observed between roots and stems or between early- and later-formed wood of the same plant, others may reflect taxonomic disparities of a high order. The pattern is represented in all three localities. Because of the close similarity, only the first specimen is illustrated.

CASG 60122

FIGURES 14–16.

MATERIAL. Secondary wood 2.5 cm. in diameter in transverse section. The angle of divergence of the rays suggests that the fragment may have been near the pith. Growth rings are not evident.

Secondary xylem. Pores solitary, angular, with a slight tendency to radial alignment, average radial diameter 100 μm. (64–128), average tangential diameter 80 μm. (58–99). Perforation plates scalariform, bars average 17 (10 to 30); average length of vessel elements 1171 μm. (986–1232); intervessel pits opposite, transitional in vicinity of perforation plates, very small; pits on tangential walls few, scattered; pits to ray cells small, numerous. Parenchyma not abundant, mostly apotracheal diffuse. Rays 3 or 4 cells wide, heterocellular, some vertically joined by uniseriate margins composed of upright cells; cross walls of upright cells oblique, sheath cells common; uniseriates 1 to 4 cells high, cells upright. Fiber pits small, numerous, apertures included.

LOCALITY. Del Puerto Creek, locality 1.

CASG 60127

MATERIAL. Fragment of mature secondary xylem 4 cm. by 2.5 cm. in transverse section. Growth rings not evident.

Secondary xylem. Pores large, solitary, average radial diameter 142 μm. (58–203), average tangential diameter 93 μm. (58–133). Perforation plates scalariform, 30 to 50 bars. Length of vessel elements average 2024 μm. (1400–2436). Parenchyma abundant, apotracheal diffuse. Rays heterocellular with high uniseriate margins, multiseriate portion of low procumbent cells, 3 or 4 cells wide, many joined vertically by uniseriate margins; uniseriates 14 or more cells high, cells upright.

LOCALITY. Del Puerto Creek, locality 1.

CASG 60208

MATERIAL. Small stem 1 cm. in diameter with large pith and only a small amount of secondary xylem.

Secondary xylem. Pores mostly solitary, diffuse, slightly angular, average radial diameter 97 μm. (58–116), average tangential diameter 71 μm. (58–87). Perforation plates scalariform, bars average 30 (up to 50), plates very oblique. Intervessel pits opposite-transitional; average vessel element length 655 μm. (580–754). Parenchyma abundant, apotracheal diffuse. Rays 1 to 6 cells wide, very high, cells square and upright. Fibers thick walled, pits bordered.

Pith. Large; with many protoxylem points and large, saclike cavities lacking epithelium. Sacs slightly elongated vertically with no interconnection or contents. The sacs could be interpreted as lysigenous, rhexigenous, or the result of postmortem microbial activity.

LOCALITY. Del Puerto Creek, locality 1.

CASG 60124

MATERIAL. A fragment of secondary xylem 1.5 cm. by 2 cm. in transverse section. Secondary walls absent in most cells. Growth rings not observed.

Secondary xylem. Pores solitary, large, average radial diameter 102 μm. (86–128), average tangential diameter 82 μm. (72–100). Perforation plates scalariform, 25 to 30 bars. Intervessel pits large, opposite; pits to ray cells similar or laterally elongated; pits to axial parenchyma round; average length of vessel elements 1062 μm. (858–1187). Parenchyma apotracheal diffuse, abundant. Rays heterocellular, 3 or 4 cells wide, numerous, uniseriate margins mostly 1 to 3 cells high, cells upright; cells of multiseriate portion square or procumbent, sheath cells common. Fibers with bordered pits, apertures included.

LOCALITY. Black Gulch, locality 2a.

CASG 60126

MATERIAL. Stem or root 5 cm. in diameter. Growth rings absent.

Secondary xylem. Pores large, oval, solitary, average radial diameter 157 μm. (114–200), average tangential diameter 89 μm. (78–143). Perforation plates scalariform, 30 to 40 bars. Average length of vessel elements 1624 μm. (1276–1850); tyloses. Parenchyma abundant, apotracheal diffuse. Rays heterocellular, up to 5 cells wide, with high uniseriate margins, cells square and upright, some connected by uniseriate margins; uniseriates up to 20 cells high, cells upright. Rhomboidal crystals occasional.

LOCALITY. Black Gulch, locality 2a.

CASG 60125

MATERIAL. Secondary xylem 1.5 cm. by 3 cm. in transverse section. Curvature of the periphery of the section coincides with demarcation of growth increment and indicates outer edge was about 2 cm. from center of axis. Growth rings indistinct.

Secondary xylem. Pores mostly solitary with some clusters of 3, average radial diameter 147 μm. (70–203), average tangential diameter 118 μm. (75–158). Perforation plates scalariform, bars average 30 (18 to 70), very oblique. Intervessel pits opposite, transitional in smaller vessels; pits to ray cells small, numerous; average length of vessel elements 1507 μm. (986–2030); tyloses. Parenchyma abundant, apotracheal diffuse. Rays heterocellular, high, many vertically joined by uniseriate margins; margins 4 to 8 cells high, sheath cells in some; uniseriates up to 20 cells high, cells upright; rhomboidal crystals occasional. Fibers with numerous bordered pits.

LOCALITY. Black Gulch, locality 2a.

CASG 60128

MATERIAL. Stem 5 cm. in diameter. Growth rings absent.

Secondary xylem. Pores solitary, large, angular, average radial diameter 114 μm. (87–145), average tangential diameter 75 μm. (70–104). Perforation plates scalariform, bars average 25 (16 to 40). Intervessel pits scarce, opposite to transitional in ligules; pits to ray cells scalariform; pits to parenchyma small; average length of vessel elements 928 μm. (580–1160); tyloses abundant. Parenchyma abundant, apotracheal diffuse, cells with dark contents. Rays heterocellular, 2 to 4 cells wide; multiseriate portion in tangential view scarcely wider than uniseriate margins, many connected vertically by margins; margins several cells high, the cells upright, square, or short procumbent; uniseriates 3 to 16 cells high, cells upright; rays variable in height, true uniseriates infrequent. All cells with dark contents. Fibers with bordered pits, apertures included, contents dark colored.

LOCALITY. Unnamed site, locality 2b.

The only specimens of this group that contain crystals are CASG 60125 and CASG 60126, collected from locality 2a. They are closely similar to CASG 60128, from locality 2b, but in this specimen the imperforate elements contain dark, amorphous inclusions. CASG 60124 (locality 2a) lacks both crystals and dark inclusions, but like CASG 60128 it has large vessel–ray pits, while in CASG 60125 they are small (none was observed in CASG 60126). In locality 1, two extremes in length of vessel elements occur: the shortest (avg. 655 μm.) in CASG 60208, a young stem; the longest (avg. 2024 μm.) in CASG 60127, mature wood. Moreover, perforation plates in CASG 60122 (also from locality 1) have the lowest number of bars (as well as the least amount of parenchyma) of any specimen among the seven. It is not unlikely that CASG 60208 and CASG 60127 represent different stages of stem development in the same species, while CASG 60122 is unrelated. Specimen CASG 60119 (locality 2a), described earlier, is similar to CASG 60124, but the perforation plates have many more bars.

Although these specimens are closely similar in general structure, we may be dealing with more than one taxon at the level of genus or higher. This interpretation is reinforced by circumstances under which the specimens were deposited. As will be discussed later, the estimated time span of the three localities is over a million years, or a period that may have encompassed several cycles of climatic — and hence vegetational — change. Furthermore, the basic structural pattern with the variations observed in the fossils occurs in a cluster of modern families, most notably the Dilleniaceae, Theaceae, Symplocaceae, Nyssaceae, Cornaceae, Euphorbiaceae, Daphniphyllaceae, and Buxaceae. Pollen attributable to the Symplocaceae, Nyssaceae, Cornaceae, and Buxaceae (*Sarcandra*, *Pachysandra*) has been reported from localities 1 and 2a (Chmura, 1973).

CASG 60129 FIGURES 21–23.

MATERIAL. A wedge of secondary xylem from a small stem or root originally at least 4 cm. in diameter. The transverse view indicates that the specimen was close to the center of the axis. Growth rings absent.

Secondary xylem. Pores solitary, oval, average radial diameter 122 μm. (87–145), average tangential diameter 75 μm. (58–87). Perforation plates scalariform, bars average 40 (30 to 60). Intervessel pits opposite, small; pits to ray cells similar; average vessel element length 765 μm. (580–986). Parenchyma abundant, apotracheal diffuse. Multiseriate portion of rays 3 cells wide, cells mostly procumbent; height of uniseriate margins variable, 1 to several cells, cells square and upright; uniseriates 2 to 10 cells high, cells upright.

LOCALITY. Del Puerto Creek, locality 1.

Uniseriate rays are abundant in transverse section near what was probably the primary xylem. Multiseriates begin at various distances from this part of the section and increase in number toward the outer edge. Changes in structure are also reflected in the presence of lower multi-

seriates with fewer rows of marginal cells in the outer portion. The mature rays may have been of this type. The wood pattern is common to several families. Examples are species of *Cornus* (Cornaceae), *Leplacea* (Theaceae), and *Weinmannia* (Cunoniaceae).

CASG 60131 FIGURES 28–31.

MATERIAL. Fork of branching axis originally at least 3 cm. in diameter.

Secondary xylem. Pores mostly solitary, some groups of 2 or 3, average radial diameter 75 μm. (46–87), average tangential diameter 69 μm. (52–87). Perforation plates scalariform, up to 30 bars. Intervessel pits opposite and, at least near ends of elements, occasionally scalariform, mostly small, round; pits to ray cells horizontally elongated; average vessel element length 754 μm. (580–812); tyloses common, thin walled. Parenchyma apotracheal diffuse. Multiseriate rays mostly 5 or 6 cells wide, the cells thick walled, mostly square and short procumbent with usually one marginal row of square cells, some rays narrow with several rows of marginal upright cells; uniseriates low, 2 to 5 upright cells. Fibers thick walled, the pits slitlike, small, bordered. All cells contain dark, amorphous inclusions.

Pith. Small, squarish; with plates of sclereids. Medullary rays extend into xylem as multiseriates.

LOCALITY. Black Gulch, locality 2a.

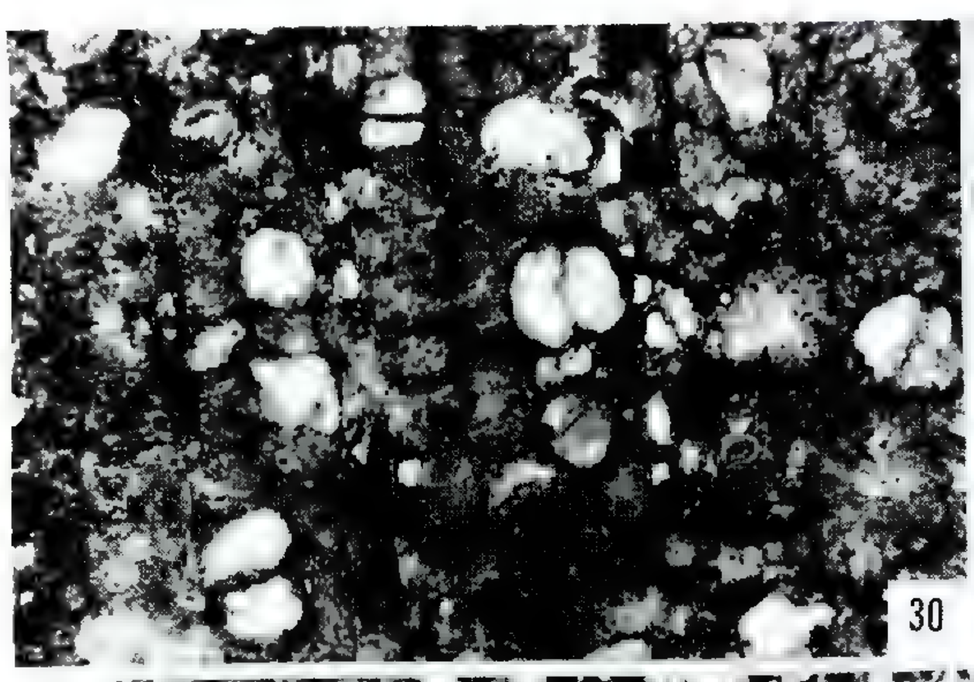
Among genera of Group IIIB section 2 with vessel elements less than 900 μm. long, the Cunoniaceae and related Eucryphiaceae are reported to have a quadrangular pith. Dark, amorphous inclusions occur in the imperforate elements in both families.

CASG 60132 FIGURES 36–39.

MATERIAL. Small stem 2 cm. in diameter. Growth rings absent.

Secondary xylem. Pores mostly solitary, angular with some radial groups of three, average radial diameter 172 μm. (87–185), average tangential diameter 87 μm. (64–127). Perforation plates scalariform, bars average 20 (10 to 29). Intervessel pits very small, numerous, opposite; pits to ray cells similar; pits in axial parenchyma numerous, small to elongated horizontally; average length of vessel elements 838 μm. (580–986). Parenchyma abundant, apotracheal diffuse. Multiseriate rays up to 15

FIGURES 30–39. 30, 31, CASG 60131: 30, transverse section, × 60; 31, longitudinal section of pith showing sclereids, × 60. 32–35, CASG 60134: 32, transverse section, × 75; 33, scalariform perforation plates, × 75; 34, radial section, × 75; 35, tangential section, × 60. 36–39, CASG 60132: 36, transverse section, × 40; 37, radial section (note abundant axial parenchyma), × 40; 38, tangential section, × 40; 39, longitudinal section of pith showing lacunae, × 4.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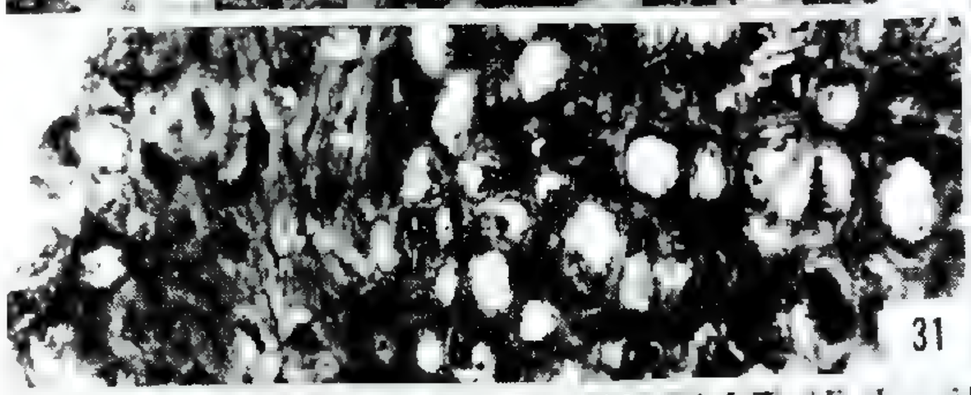
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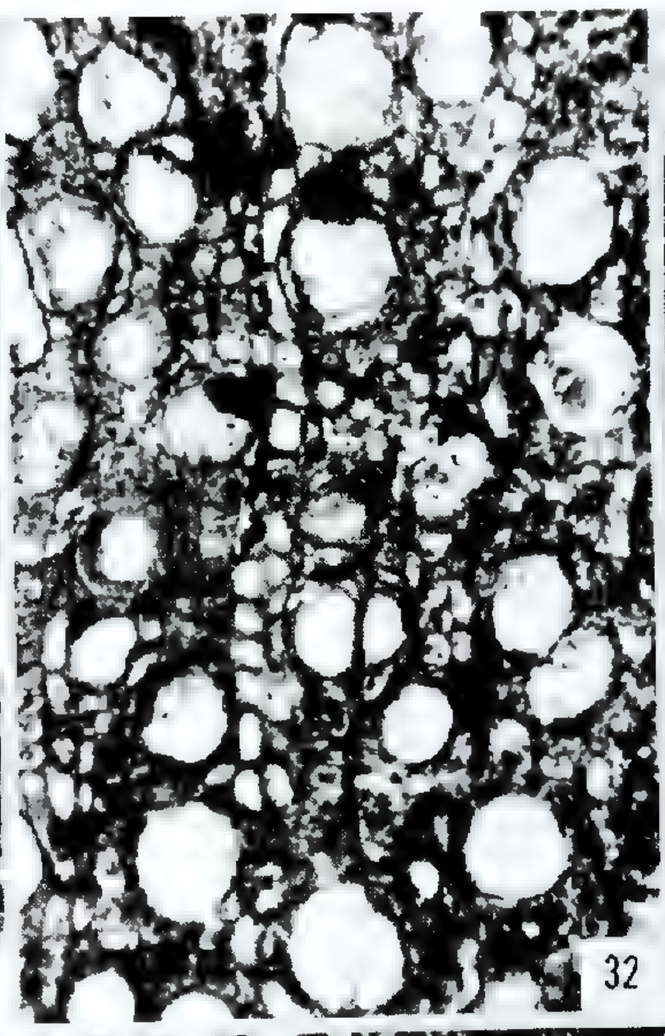
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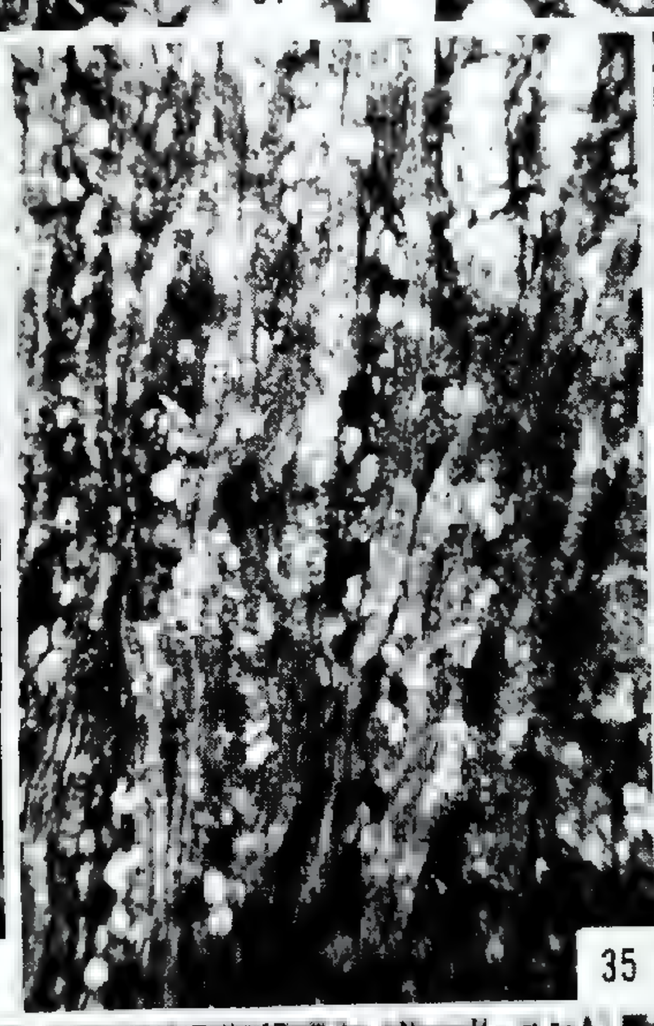
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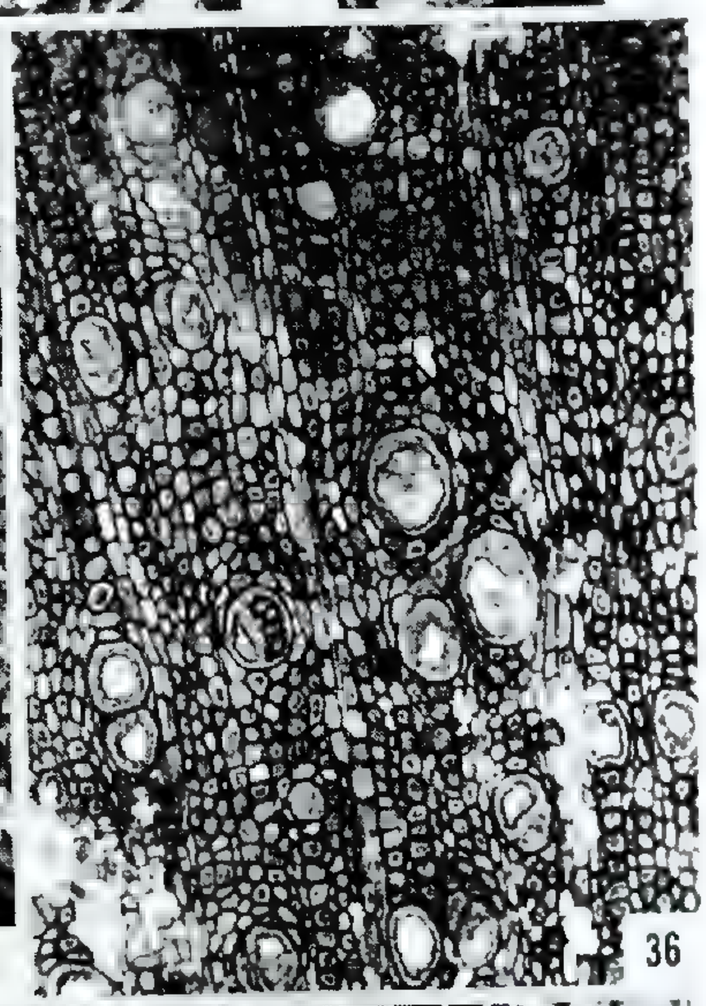
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cells wide, very high, cells mostly square or upright; uniseriates 3 to 10 cells high, cells upright. Chambered crystals in some upright cells. Fiber pits small, bordered.

Pith. Many primary xylem points separated by medullary portion of wide rays. Cells in center large, smaller at periphery.

LOCALITY. Del Puerto Creek, locality 1.

In longitudinal section the pith appears to be chambered (FIGURE 39), but the lacunae are at irregular intervals and appear to have resulted from mechanical rupture of the tissue. The wood pattern falls within the range of variation of Bailey and Howard's (1941) Group I Icacinaceae. Single rhomboidal crystals have been observed in individual ray cells in this group, but chambered crystals have not been reported. Intervessel pits in this group are not particularly small.

CASG 60134 FIGURES 32–35.

MATERIAL. Stem 2.5 cm. in diameter including a large pith.

Secondary xylem. Pores solitary, numerous, average radial diameter 73 μm. (64–77), average tangential diameter 58 μm. (58–64). Perforation plates scalariform, less than 10 (mostly 4 or 5) widely spaced bars. Intervessel pits opposite to almost alternate, some laterally elongated; pits to ray cells large, laterally elongated; average length of vessel elements 476 μm. (3 measurements only); thin-walled tyloses common. Parenchyma apotracheal diffuse. Multiseriate rays 2 or 3 cells wide, cells square and short procumbent. Fibers thick walled, the pits numerous, large, flattened.

Pith. Over 1 cm. in diameter; cells near primary xylem thick walled, those in interior thin walled.

LOCALITY. Black Gulch, locality 2a.

Proper tangential sections were not obtained except near the pith. Convoluted, thick-walled, hyphaelike cells occupy a portion of the pith and can be confused with the thick-walled pith cells, although the latter possess pits, while the hyphaelike cells do not. Few families that have Group IIIB section 2 type wood, perforation plates with fewer than 10 bars, and vessel elements shorter than 600 μm. also have large vessel–ray pits. The Hamamelidaceae is one of those few.

The following three specimens (CASG 60135, CASG 60206, and CASG 60207) are classified as Group IIIB section 3. Woods of some extant genera of this group with vessel elements less than 900 μm. in length and with less than 15 bars in the perforation plates are members of the Caprifoliaceae, Garryaceae, Epacridaceae, and Ericaceae. Woods with an average of more than 15 bars occur in the Ericaceae and Icacinaceae.

CASG 60135 FIGURES 40–44.

MATERIAL. Small stem 2 cm. in diameter. Growth rings apparent with magnification.

Secondary xylem. Pores small, solitary, average radial diameter 69 μm. (58–87), average tangential diameter 60 μm. (52–70). Perforation plates scalariform, bars average 15 (10 to 25). Intervessel pits small, opposite to alternate; pits to ray cells small, numerous, apertures narrow; average vessel element length 661 μm. (580–754). Parenchyma abundant with tendency toward uniseriate tangential rows. Multiseriate rays 2 or 3 cells wide, cells square and procumbent; uniseriate margins of square and upright cells; uniseriates 3 to 5 cells high, cells upright. Fiber pits small, bordered, on all walls; tracheids occasional.

Pith. Oblong in transverse view.

Phloem. Cells mostly thin walled with staggered small patches of large stone cells. Rhomboidal crystals common in parenchyma.

LOCALITY. Unnamed site, locality 2b.

Pyrite obscures most of the cells in this specimen. Wall pits are preserved in many areas, but it is often difficult to determine whether they are parenchyma, ray, tracheid, or vessel pits. Pits that are definitely on intervessel walls are small and tend to be somewhat laterally elongated. There is a tendency to an alternate arrangement in some areas. Pits on the walls of fibers, ray cells, and what are interpreted as tracheids have oblique apertures (FIGURE 43).

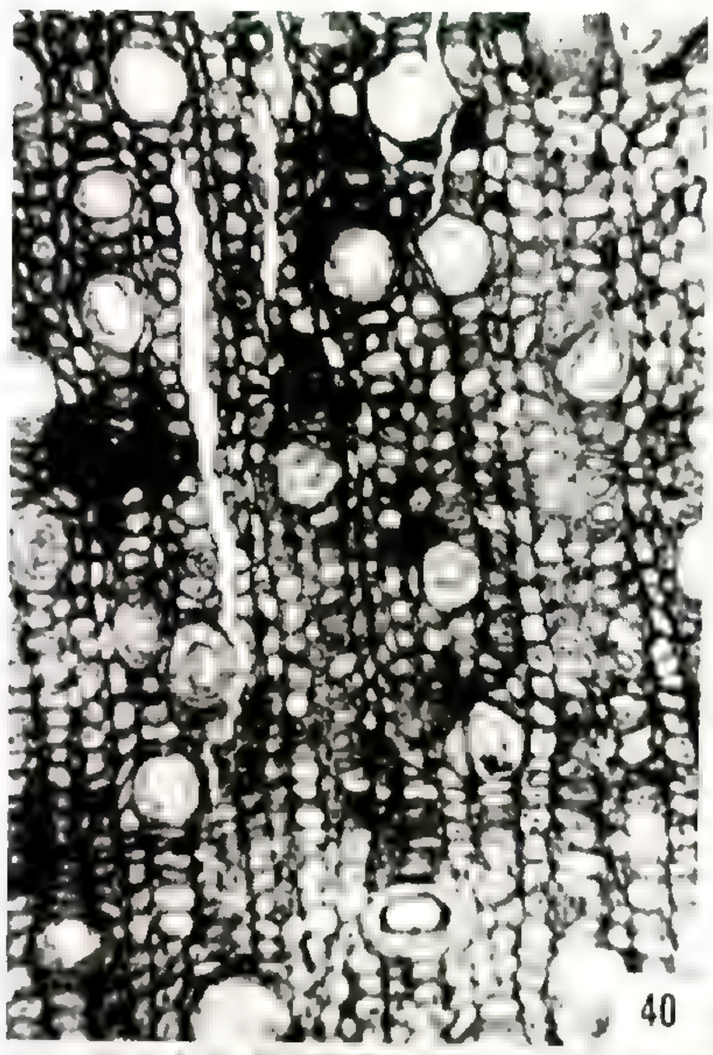
The general pattern is similar to that of woods of species of the Ericaceae. Tracheidlike elements are occasionally associated with vessels in this family. The oblong pith in the fossil suggests that the plant had opposite leaves; in fact, one section shows two branch traces departing from opposite sides of the pith. Some Ericaceae have opposite phyllotaxy.

CASG 60206 FIGURES 45, 46.

MATERIAL. Stem 2.5 cm. in diameter.

Secondary xylem. Pores solitary, small, average radial diameter 53 μm. (36–71), average tangential diameter 48 μm. (36–57). Perforation plates scalariform with an average of 24 (20 to 40) coarse bars. Intervessel pits opposite to mostly alternate, numerous, small; pits to ray cells small, round; average length of vessel elements 608 μm. (580–928). Parenchyma apotracheal diffuse, abundant. Multiseriate rays 3 or 4 cells wide, cells variable in size and shape; uniseriate margins from one to many cells high, cells upright; uniseriates numerous, the cells high, upright. Fibers thick walled, the pits small, bordered.

Pith. Large; cells large.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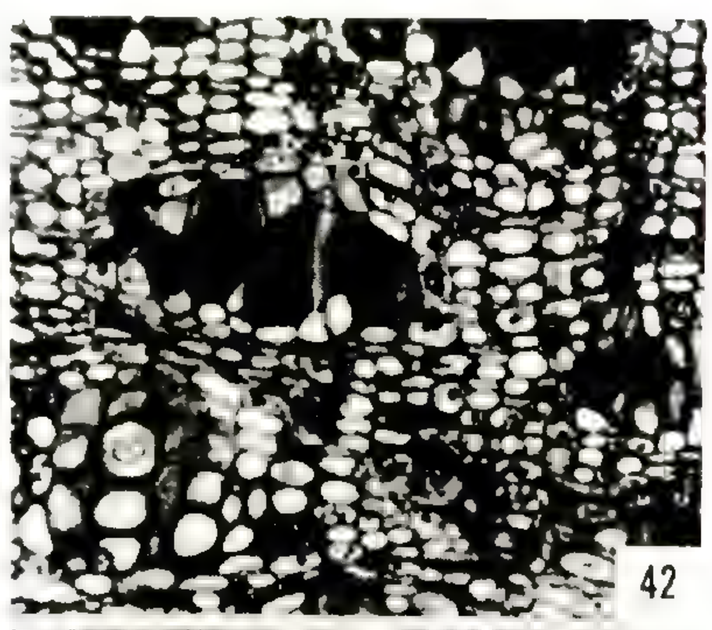
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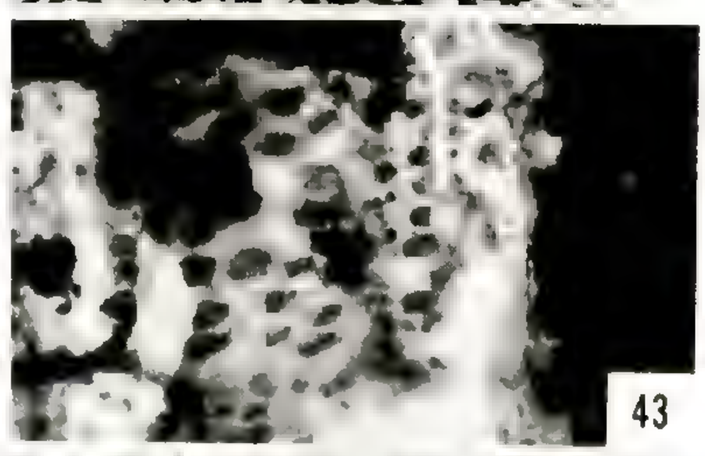
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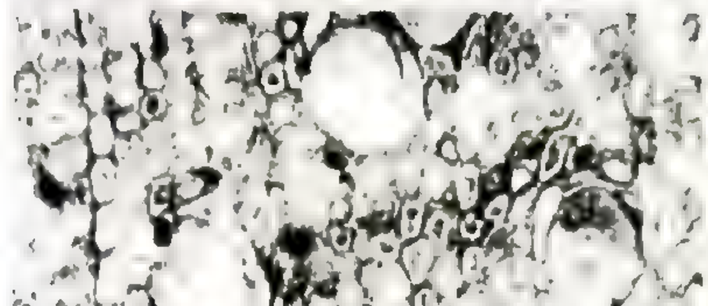
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Phloem. Sclereids arranged in irregular tangential lines.

LOCALITY. Del Puerto Creek, locality 1.

High, broad rays, prominent in one part of the tangential section, may be associated with a branch. Individual imperforate vascular elements occur within the rays. The wood pattern has some features in common with certain Cornaceae, Ericaceae, and Icacinaceae (*Apodytes*).

CASG 60207 FIGURES 47–49.

MATERIAL. Small stem with pith. Growth rings indistinct.

Secondary xylem. Pores mostly solitary with occasional clusters of 3, slightly angular to rounded, average radial diameter 74 μm. (57–94), average tangential diameter 58 μm. (50–64). Perforation plates scalariform, bars average 12 (4 to 38). Intervessel pits rare, opposite to alternate in ligules, laterally elongated and arranged in loose vertical files in some; pits to ray cells numerous, small, arrangement random; average vessel element length 657 μm. (626–1550). Parenchyma diffuse. Multiseriate rays 2 to 4 cells wide with high uniseriate margins of high upright cells, cells of multiseriate portion procumbent, many rays vertically joined by uniseriate margins; uniseriates 10 to 15 cells high, cells upright and square; rays near pith uniseriate, becoming biseriate and multiseriate in later-formed wood. Fibers thick walled with bordered pits on all walls.

Pith. Small; cells large and round in transverse section, flattened in long section. Primary xylem points separated from pith cells by groups of fibers.

LOCALITY. Black Gulch, locality 2a.

The wide range in length of vessel elements, as well as the differences between rays in early- and later-formed wood, indicates that the stem was in a transitional stage of maturation. This pattern could be typical of young stems of a number of Group IIIB families in which the vessel elements are longer than 1 mm. in the mature wood, such as the Cornaceae, Icacinaceae, and Caprifoliaceae.

ACKNOWLEDGMENTS

I am indebted to Elso Barghoorn for providing facilities to work with the Harvard Wood Collections and for other courtesies; to Robert Koep-

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FIGURES 40–49. 40–44, CASG 60135: 40, transverse section, × 80; 41, tangential section, × 80; 42, transverse section of outer phloem (note patches of large stone cells), × 75; 43, pits of ray cell, × 300; 44, radial section, × 80. 45, 46, CASG 60206: 45, transverse section, × 45; 46, tangential section, × 40. 47–49, CASG 60207: 47, transverse section, × 70; 48, radial section, × 75; 49, tangential section, × 45.

pen for assistance in procuring wood specimens as well as for providing space to work at the Forest Products Laboratories, Madison, Wisconsin; and to the Forestry Department, Oxford University, England, for providing facilities to study its wood collection. Special thanks are due the Department of Biological Sciences, Stanford University, for the use of laboratory space and for many other special privileges. Financial support was received from the National Science Foundation (GB-184 and GB-8168), the American Philosophical Society, and the RESA Foundation. Thanks are extended to Jack Wolfe of the U. S. Geological Survey, Menlo Park, California, and to Sherwin Carlquist, Rancho Santa Ana Botanic Garden, Claremont, California, for reading an earlier version of the present paper.

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FOLIAR TRICHOMES OF QUERCUS SUBGENUS QUERCUS IN THE EASTERN UNITED STATES

PAUL M. THOMSON AND ROBERT H. MOHLENBROCK

SINCE DYAL'S PUBLICATION of a key to the oaks of the eastern United States (1936), an increasing amount of attention has been paid to the trichomes that collectively contribute to foliar pubescence. Her characterization of oak trichomes included two basic types, glandular and nonglandular, and some quantitative data regarding size (the tip-to-tip extent of the rays, which she called the spread). The information was integrated with that for other vegetative features to produce a workable key to the species of *Quercus* L. as they were then understood. Trichomes have also been used as evidence to detect hybridization among species of white oaks (Tucker & Muller, 1958; Tucker, 1963; Maze, 1968; and others). These workers found that the number of ray branches and their spread conformed to the ranges of variability that could be associated with particular species. Hybridization between individuals of different species resulted in modification of these characters in a manner similar to other quantifiable characters also studied.

Because of the utility of evidence from trichome characters demonstrated by previous investigators, the present study was initiated to determine if quantifiable characters of the trichomes could be combined with the types to produce a valid set of characters for recognizing individuals of eastern white oak species. Furthermore, if the character sets proved to be uniform for the species, they could provide a basis for recognizing hybrids between them.

Most recently, trichome structure has been closely inspected by Hardin (1976), who defined ten types. Four of these fall into Dyal's glandular class, and the remaining six belong to her nonglandular group. In the glandular class, simple-uniseriate and bulbous types were found on leaves of the white oaks described here, but rosulate and simple-branched hairs were not observed. Examples of the simple-uniseriate and bulbous trichomes are pictured in FIGURES 5 and 12, respectively. Solitary (FIGURES 7, 16), fasciculate (FIGURES 2, 17), stipitate-fasciculate (FIGURES 10, 11), stellate (FIGURES 5, 15), and fused-stellate (FIGURES 12, 18) trichomes are nonglandular types that also occur. Multiradiate and appressed-lateral, nonglandular trichomes were not observed. Although Hardin's terms are more precise than Dyal's, hers are retained for convenience in referring to a trichome class in the descriptions that follow.

MATERIALS AND METHODS

Specimens for this study were obtained from herbaria of the Missouri Botanical Garden and Southern Illinois University, and from collections

by one of us (Thomson) from nine states over the past four years. In all, approximately 2000 specimens were utilized. From these, 50 were chosen from each species for assessment of trichome types and for obtaining the quantitative data, i.e., number of rays and ray spread. Specimens were selected to insure the broadest possible representation of the known extent of range and habitats of the species. These selected specimens served as the basis upon which characterization was established.

Trichomes were viewed with a light microscope at 100× using reflected light. All measurements were taken from trichomes occurring on the abaxial surface of leaves midway between base and apex and midvein and margin, and were done with an eyepiece micrometer. In an effort to avoid unwittingly choosing certain types over others, counts were made for those nearest the ten numbers of the ocular micrometer when superimposed. If more than one type was encountered, measurements were taken for ten of each. Range and mean were determined for number of rays per trichome and for spread (in mm.) for 500 trichomes of each species. A range for means of trichomes of individual leaves ($\bar{X}$ range) was also calculated for the two characters. Measurements were not made for glandular hairs.

All remaining specimens were viewed, and counts and measurements from three trichomes for each were compared to range and mean values established in the initial survey. Thus, the number of trichomes contributing to the establishment of the descriptive statistics varied from 500 for *Quercus alba* to 833 for *Q. macrocarpa* (50 specimens multiplied by 10 trichomes plus 111 additional specimens multiplied by 3 trichomes). One exception to this was *Q. oglethorpensis*, for which only ten specimens were available. However, because the species has a very limited distribution (Duncan, 1950), the values obtained are considered at least as representative of that taxon as were the 161 specimens of the comparatively far-ranging *Q. macrocarpa*. A summary of quantitative data for nonglandular trichomes by species is presented in TABLE 1. Values are not given for the solitary type hair since, by definition, it has only a single axis and no spread.

Scanning electron micrographs were prepared to show trichomes that are believed, from these data, to be representative of the species. Tissues were cut from leaves with a cork borer and fixed in cold (4°C) 3 percent glutaraldehyde in veronal buffer (pH 7.4) for two hours. After fixing, the tissues were washed twice with buffer for 15 minutes at 4°C and then fixed in 1 percent aqueous osmium tetroxide at 4°C for 30 minutes. Specimens were serially dehydrated in ethyl alcohol, further dehydrated in freon, critical point dried, and vacuum evaporated with carbon.

Species included in this study were: *Quercus alba, Q. austrina, Q. bicolor, Q. chapmanii, Q. durandii, Q. geminata, Q. lyrata, Q. macrocarpa, Q. margaretta, Q. minima, Q. montana* (*Q. prinus* auct., non Linnaeus), *Q. oglethorpensis, Q. prinoides* Willdenow, including var. *prinoides* and var. *acuminata* (*Q. muehlenbergii*), *Q. prinus* (*Q. michauxii* of some authors), *Q. stellata*, and *Q. virginiana*.

TABLE 1. Range, mean, and mean range for quantitative features of nonglandular trichomes of the eastern white oaks.

Species	Types	Spread (mm.)			Number of rays		
		Range	$\bar{X}$	$\bar{X}$ Range	Range	$\bar{X}$	$\bar{X}$ Range
Quercus alba	solitary						
	fasciculate	0.17-0.24	0.22	0.17-0.26	3- 8	5.1	4.5- 6.7
austrina	solitary						
	fasciculate	0.20-0.50	0.31	0.21-0.39	2- 9	5.0	4.2- 6.2
bicolor	fasciculate	0.30-0.65	0.53	0.36-0.55	2- 8	4.2	3.5- 5.1
	stellate	0.07-0.22	0.15	0.09-0.18	6-16	10.0	5.6-13.2
chapmanii	fasciculate	0.10-0.25	0.18	0.13-0.23	4- 9	6.8	5.1- 7.5
durandii	fasciculate	0.15-0.35	0.23	0.19-0.28	4- 9	6.5	4.9- 8.3
	stellate	0.10-0.20	0.14	0.11-0.18	8-16	12.6	7.3-13.6
geminata	stipitate, fused-stellate	0.20-0.45	0.29	0.24-0.33	7-17	11.1	8.6-13.7
	fused-stellate	0.14-0.21	0.15	0.12-0.19	8-14	11.5	11.0-16.5
lyrata f. *viridis*	solitary						
	fasciculate	0.10-0.30	0.20	0.11-0.19	2- 4	2.5	1.0- 3.0

f. lyrata	solitary						
	fasciculate	0.10-0.33	0.21	0.16-0.28	2- 6	3.4	2.8- 4.0
	stellate	0.10-0.22	0.12	0.09-0.24	6-16	10.1	6.5-12.2
macrocarpa	fasciculate	0.20-0.60	0.33	0.26-0.50	2- 9	4.6	3.4- 5.1
	stellate	0.10-0.26	0.14	0.12-0.25	4-16	7.8	6.2-10.6
margaretta	stipitate-fasciculate	0.40-1.00	0.64	0.40-0.77	4- 9	6.7	5.2- 8.2
minima	sessile, fused-stellate	0.07-0.19	0.12	0.10-0.15	7-17	12.6	7.5-17.8
montana	stipitate-fasciculate	0.10-0.25	0.14	0.16-0.29	2- 5	3.1	2.8- 4.3
	fasciculate	0.08-0.25	0.16	0.11-0.30	1- 5	2.4	1.9- 2.7
oglethorpensis	stipitate-fasciculate	0.20-0.40	0.32	0.25-0.37	3- 9	6.3	4.5- 7.9
prinoides							
var. prinoides	stellate	0.09-0.22	0.15	0.09-0.20	6-16	10.2	8.0-13.0
var. acuminata	stellate	0.09-0.22	0.15	0.11-0.21	6-16	9.2	7.1-12.0
prinus	solitary						
	fasciculate	0.20-0.45	0.33	0.22-0.39	2- 8	3.4	2.0- 4.9
stellata	fasciculate	0.15-0.49	0.31	0.20-0.39	4- 9	6.6	4.0- 8.7
virginiana							
var. virginiana	sessile, fused-stellate	0.06-0.18	0.11	0.09-0.16	9-18	15.6	13.6-16.5
var. fusiformis	sessile, fused-stellate	0.08-0.16	0.12	0.09-0.17	12-24	17.1	14.2-18.3

FOLIAR TRICHOMES OF THE EASTERN WHITE OAKS

Quercus alba Linnaeus

The leaves of white oak have usually been described as glabrous. In this study, however, three types of trichomes were observed. On the leaf surface minute, appressed, glandular hairs occur. These are typical for *Quercus alba*. Solitary, nonglandular hairs are occasionally found on the midvein. These may be associated with a yellowish, fasciculate hair occurring near the midvein, especially in vein axils. The trichomes do not always occur together. Most specimens had glandular hairs only, but some had both these and the nonglandular trichomes.

Fasciculate hairs of white oak have ray branches appearing twisted and flattened and are attached to epidermal cells that are slightly elevated from the surface, forming a pedestal. The rays extend an average of 0.22 mm. (range 0.17–0.24 mm.) and are 3 to 8 ($\overline{X}$ = 5.1) per trichome. Fasciculate hairs are numerous on young leaves but are shed as the leaf matures. Approximately 15 percent of the specimens of this study retained the hairs in the midvein area. The dehydrated appearance of the rays is presumably due to the fact that the cell walls are thinner than those of fasciculate hairs of the other eastern oaks that possess them (FIGURE 1). Solitary hairs vary from 0.14 to 0.29 mm. in length.

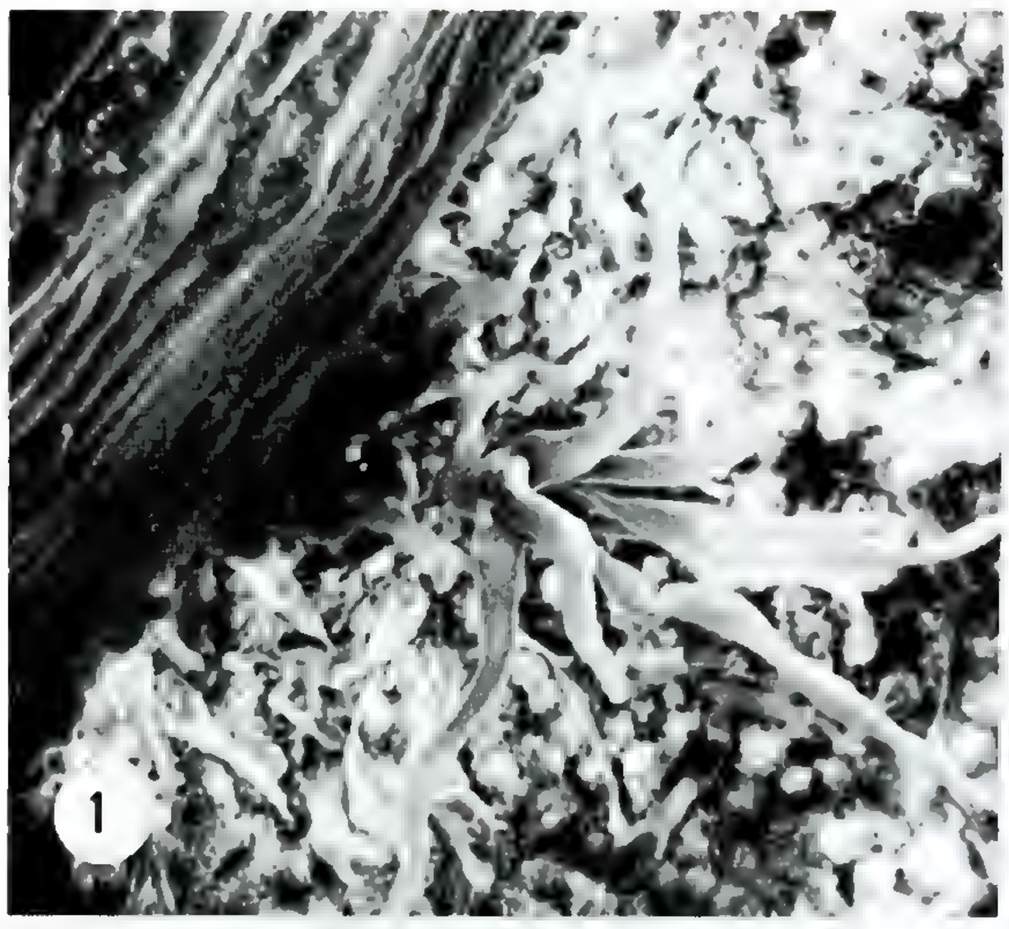
Quercus austrina Small

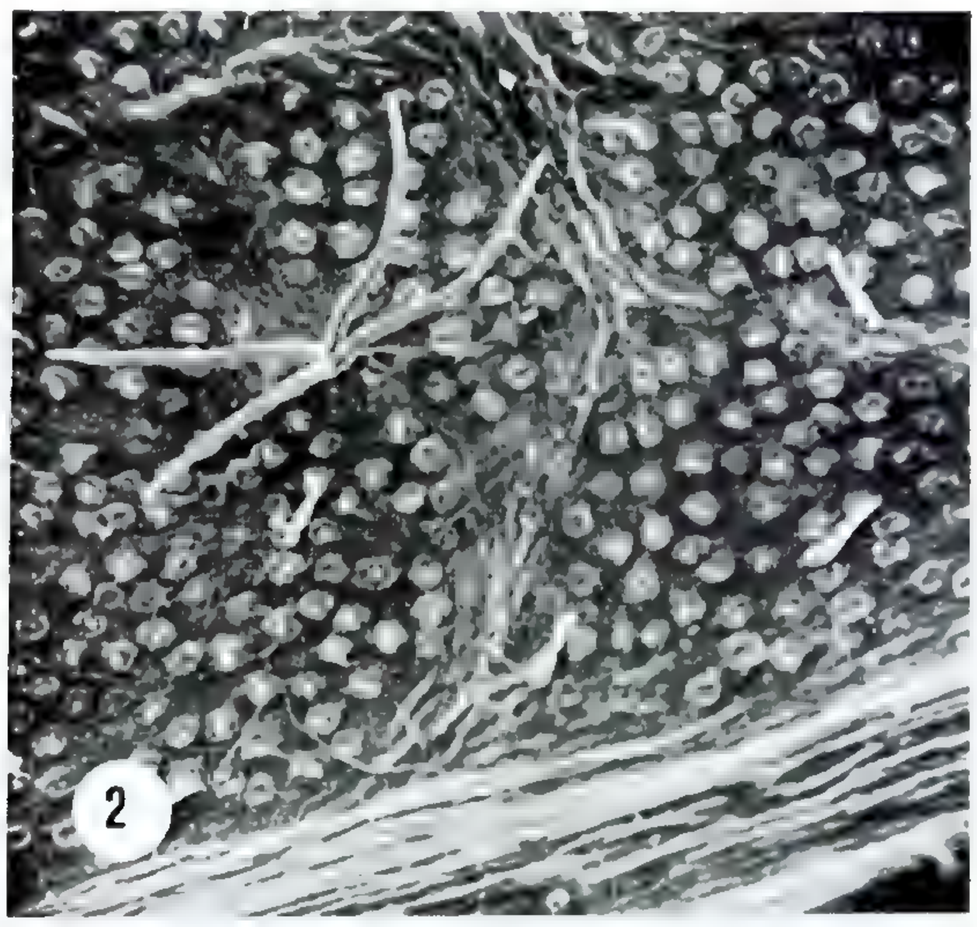
Nonglandular trichomes of bluff oak are restricted to the midvein area and are of both solitary and fasciculate types. Solitary hairs are more frequent than fasciculate trichomes, but both are fairly infrequent. Occurring on or near the midvein, the fasciculate type is pedestaled and yellow; it has a spread of 0.20–0.50 mm. ($\overline{X}$ = 0.31 mm.) and 2 to 9 rays ($\overline{X}$ = 5.0 rays). Solitary hairs vary from 0.20 to 0.40 mm. in length ($\overline{X}$ = 0.29 mm.) and are restricted to the midvein. Glandular hairs occur on the leaf surface between the principal veins and are simple-uniseriate, appressed, one- to three-celled, and yellowish. In their distribution, their types, and their size, the trichomes (FIGURE 2) are generally most similar to those of *Quercus alba*.

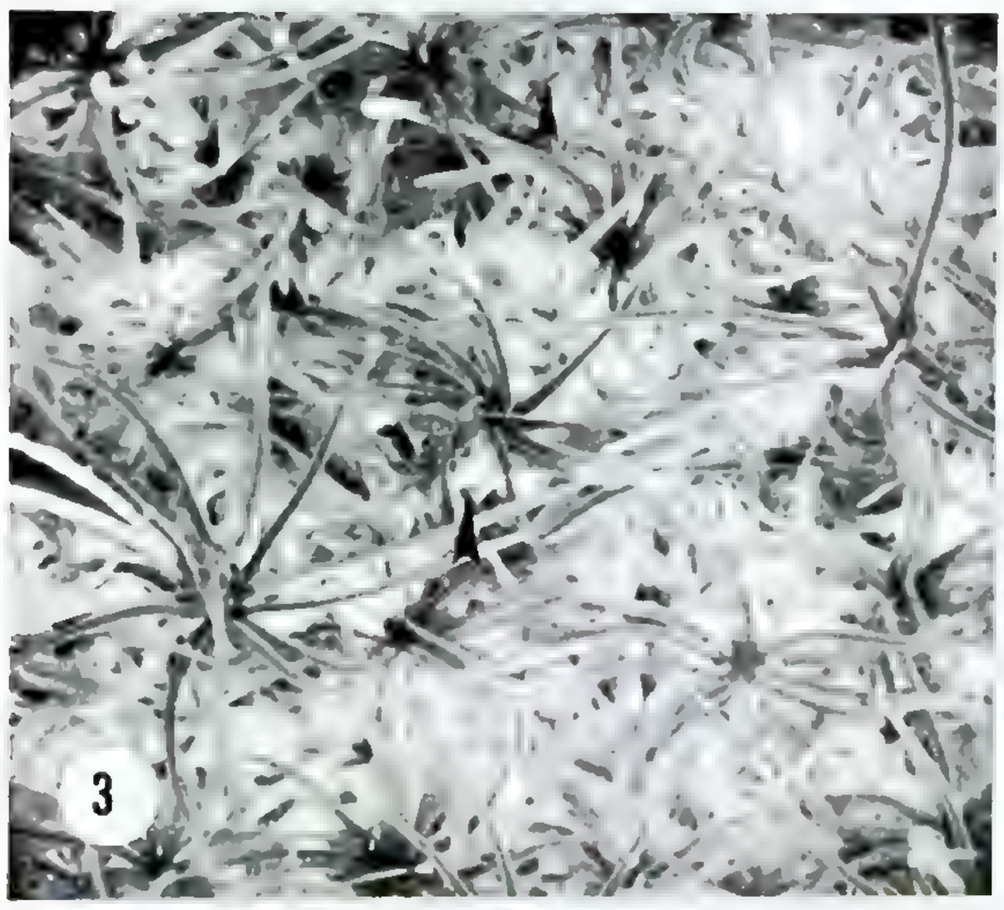
Quercus bicolor Willdenow

Swamp white oak possesses one of the most characteristic combinations of glandular and nonglandular trichomes among the white oaks. Nonglandular hairs are fasciculate and stellate. The fasciculate hairs are erect with 2 to 8 rays ($\overline{X}$ = 4.2) and a spread of 0.30–0.65 mm. ($\overline{X}$ = 0.53 mm.); they occur uniformly over the leaf surface. The stellate trichomes are appressed or looser with 6 to 16 rays ($\overline{X}$ = 10.0) and have a spread of 0.07–0.22 mm. ($\overline{X}$ = 0.15 mm.). Both of these types are whitened, but among them are erect, bulbous, glandular hairs that are red. These tend to become dark brown in pressed specimens (FIGURE 3).

Most specimens are quite densely pubescent, but *Quercus bicolor* var.







FIGURES 1–6: 1, *Quercus alba*, fasciculate hair, × 400; 2, *Q. austrina*, fasciculate hair, × 135; 3, *Q. bicolor*, fasciculate and stellate hairs, × 200; 4, *Q. chapmanii*, fasciculate hair, × 270; 5, *Q. durandii*, fasciculate and stellate hairs, × 135; 6, *Q. geminata*, stipitate, fused-stellate and sessile, fused-stellate hairs, × 200.

mollis Nutt., a variety with green leaves, has been described. In the few specimens of that taxon studied, no difference in trichome types was observed, although density of all was reduced.

Quercus chapmanii Sargent

Both glandular and nonglandular trichomes are present on the leaves of Chapman's oak. Simple-uniseriate, glandular hairs are minute, appressed, and yellow, and occur on the surface between principal veins. Often these are dense enough to color the leaf. The nonglandular trichome is considered fasciculate, although the rays tend to diverge in roughly the same plane. Pedestaled and yellow, it occurs on or near the midvein and primary veins. Rays vary from 4 to 9 ($\overline{X}$ = 6.8) and have a spread of 0.10–0.25 mm. ($\overline{X}$ = 0.18 mm.) (FIGURE 4).

Quercus durandii Buckley

Two sizes of nonglandular hairs occur on leaves of Durand's oak. The larger type is like that found on *Quercus austrina*. It is fasciculate, pedestaled, and yellow and occurs on or near the midvein and principal veins. Rays vary from 4 to 9 ($\overline{X}$ = 6.5) and measure 0.15–0.35 mm. ($\overline{X}$ = 0.23 mm.) across. The smaller type is stellate and measures 0.10–0.20 mm. ($\overline{X}$ = 0.14 mm.), but is more branched (8 to 16 rays averaging 12.6 branches per hair). Whitened and appressed, these occur on the leaf surface. FIGURE 5 shows both types.

Quercus geminata Small

This oak has been treated both as a variety of *Quercus virginiana* (var. *maritima* (Michaux) Sargent) and as a separate species. Its status is not something that this study intends to resolve; however, the trichome structure seems to us to differ sufficiently from that of *Q. virginiana* to warrant distinction.

Two sizes of nonglandular, fused-stellate hairs are present on leaves of *Quercus geminata* (FIGURE 6). The larger size occurs on the principal and lesser veins. Beyond the area of fusion, the rays are free and range from 7 to 17 per hair ($\overline{X}$ = 11.1) with a spread of 0.20–0.45 mm. ($\overline{X}$ = 0.29 mm.). The hairs are yellow or occasionally red in their centers. Beneath the larger hairs are smaller ones, 0.14–0.21 mm. ($\overline{X}$ = 0.15 mm.) across, which are appressed or slightly ascending. The hairs have 8 to 14 rays ($\overline{X}$ = 11.5) and are fused only near the base. Both sizes of trichomes are whitened in appearance.

The differences in trichomes for *Quercus geminata* and *Q. virginiana* are of an order typically seen only between distinct species.

Quercus lyrata Walter

With respect to trichome structure two leaf forms are known for overcup oak. One is a low-density form in which the leaf appears green to the unaided eye (f. *viridis* Trelease). Trichomes are nonglandular, erect, and either solitary or fasciculate and 2- to 4-rayed. Approximately half of the

specimens were observed to have a combination of solitary and 2-rayed hairs, while the remainder possessed these and 3- and 4-rayed forms. Overall, trichomes have 1 to 4 rays ($\overline{X} = 1.5$), with fasciculate hairs (2 to 4 rays) spreading 0.10–0.30 mm. ($\overline{X} = 0.20$ mm.). The hairs are distributed along the midvein and primary veins but occasionally arise from veinlets (FIGURE 7).

The second form (f. *lyrata*) is densely pubescent with two sizes of nonglandular hairs. The larger are solitary or fasciculate, yellow, and 2- to 6-rayed ($\overline{X} = 3.4$), with a spread of 0.10–0.33 mm. ($\overline{X} = 0.21$). The smaller are stellate, whitened, appressed or looser, with (4 to) 6 to 16 rays ($\overline{X} = 10.1$) that extend 0.10–0.22 mm. ($\overline{X} = 0.12$ mm.) (FIGURE 8). Trichomes of the dense form resemble those of *Quercus macrocarpa* in general appearance, but differ from them quantitatively (TABLE 1).

Quercus macrocarpa Michaux

Burr oak has nonglandular trichomes of two distinct size ranges. The larger are fasciculate with a spread of 0.20–0.60 mm. ($\overline{X} = 0.33$ mm.) and possess 2 to 9 rays, averaging 4.6 per trichome. Beneath these are smaller, stellate hairs measuring 0.10–0.26 mm. ($\overline{X} = 0.14$ mm.) across and having 4 to 16 rays, which average 7.8 per trichome. These are whitened and may be appressed or looser. Occasionally the nonglandular hairs are associated with simple-uniseriate, glandular, yellow ones (FIGURE 9).

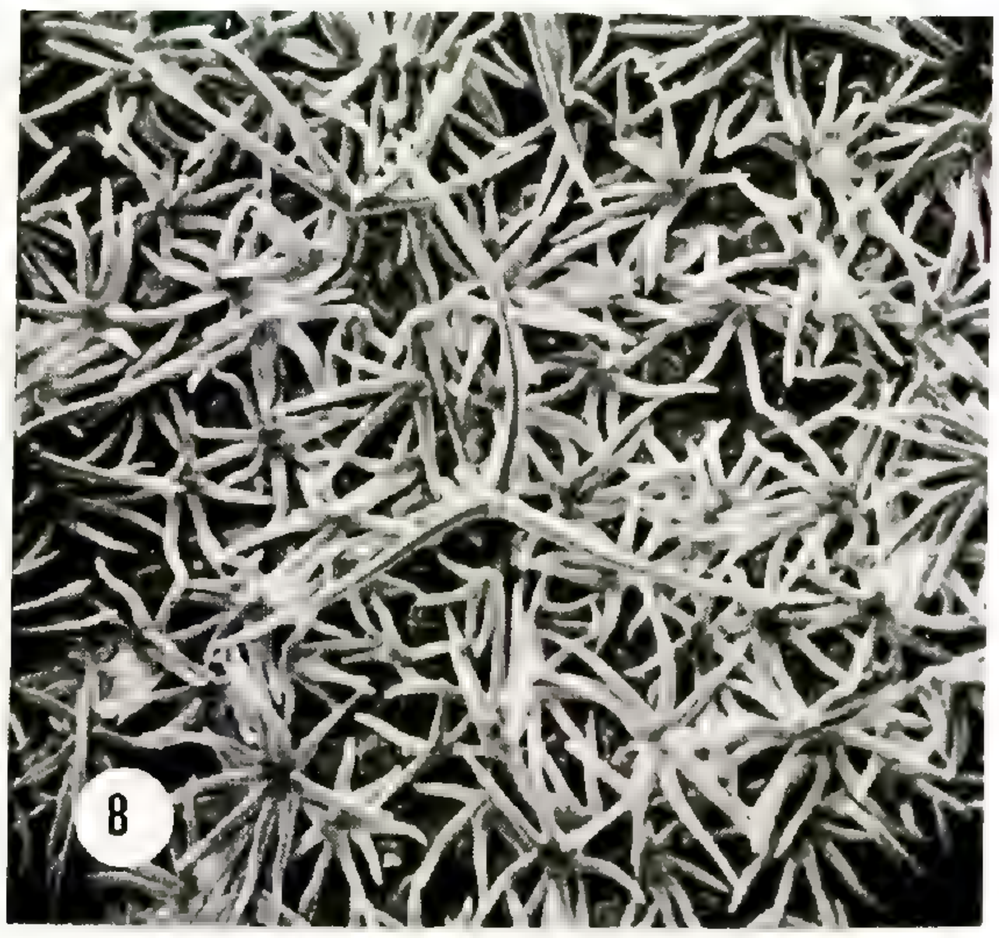
On approximately 10 percent of the specimens, only the larger trichomes are found. In such cases they are typically longer and have a greater spread than when they occur with the smaller form. We have no data from field studies with which to correlate this form to determine if it has ecological significance.

Quercus margaretta Ashe

In leaf form *Quercus margaretta* most closely resembles *Q. stellata*, but in trichome morphology the resemblance to *Q. oglethorpensis* is striking. As with Oglethorpe oak, the stipitate-fasciculate hairs arise from distinct pedestals, but they differ in size. Trichomes of *Q. margaretta* have the greatest spread of any of those of the eastern white oaks, 0.40–1.0 mm. ($\overline{X} = 0.64$ mm.). Rays range from 4 to 9 per hair and average 6.7. FIGURE 10 shows the pedestal at the base of the hair, while FIGURE 11 shows the entire hair. These are whitened or sometimes have a yellowish tint and are distributed upon veins. Simple-uniseriate hairs are also found on the leaves.

Quercus minima (Sargent) Small

Quercus minima is considered a variety of *Q. virginiana* by some taxonomists, and a distinct species by others. Little support is given the latter consideration by trichome structure, which is identical with that of *Q. virginiana*. The fused-stellate trichomes do, however, differ from those of *Q. virginiana* in number of rays and spread. Branches vary in number from



FIGURES 7–12: 7, *Quercus lyrata* f. *viridis*, solitary and fasciculate hairs, × 150; 8, *Q. lyrata* f. *lyrata*, fasciculate and stellate hairs, × 200; 9, *Q. macrocarpa*, fasciculate and stellate hairs, × 200; 10, *Q. margaretta*, stipitate-fasciculate hair showing stipe and pedestal, × 700; 11, *Q. margaretta*, stipitate-fasciculate hair seen from above, × 200; 12, *Q. minima*, sessile, fused-stellate hairs, × 250.

7 to 17 ($\overline{X}$ = 12.6) and extend 0.07–0.19 mm. ($\overline{X}$ = 0.12 mm.) (FIGURE 12). Glandular hairs are also present. Although individuals are not readily separated from *Q. virginiana* on trichome evidence, the aristate, lobed leaves and the typically shrubby habit combine to distinguish them from the live oak. The taxonomic status of this oak is in need of critical evaluation based on population studies.

Quercus montana Willdenow (*Quercus prinus* Linnaeus)

Rock chestnut oak is easily recognized by the tufted appearance of nonglandular hairs crowded into the vein axils. This pattern, although typical for many species of subgenus ERYTHROBALANUS, is unique to this species of eastern white oak. In *Quercus montana*, trichomes are attached laterally to opposing surfaces of primary veins and the midvein near their union. Density decreases sharply from the origin of vein axils to the margin, thus producing the tufted appearance. Hairs are stipitate-fasciculate, have 2 to 5 rays ($\overline{X}$ = 3.1), and are narrowly spread (0.10–0.25 mm., ($\overline{X}$ = 0.14 mm.) in spite of their length of 0.20–0.40 mm.

In addition to this trichome type, the leaf surface between primary veins contains a smaller nonglandular hair that may be erect or appressed. These hairs are solitary or are fasciculate with 2 to 5 rays ($\overline{X}$ = 2.4) that average 0.16 mm. across and vary from 0.08 to 0.25 mm. (FIGURE 13).

Quercus oglethorpensis Duncan

Oglethorpe oak, like *Quercus margaretta*, has stipitate-fasciculate, nonglandular trichomes attached to pedestals. While these species are easily separated on a variety of morphological features of the leaf (e.g., *Q. oglethorpensis* is entire, *Q. margaretta* is lobed), as well as other features, they are also distinguishable by quantitative features of their trichomes. *Quercus oglethorpensis* has 3 to 9 ray branches ($\overline{X}$ = 6.3) with a spread of 0.20–0.40 mm. ($\overline{X}$ = 0.32 mm.). Those of *Q. margaretta* are similar in ray number but average twice the spread ($\overline{X}$ = 0.64 mm.). Also, *Q. oglethorpensis* has minute, appressed, yellow, glandular hairs that are typically absent in *Q. margaretta* (FIGURE 14).

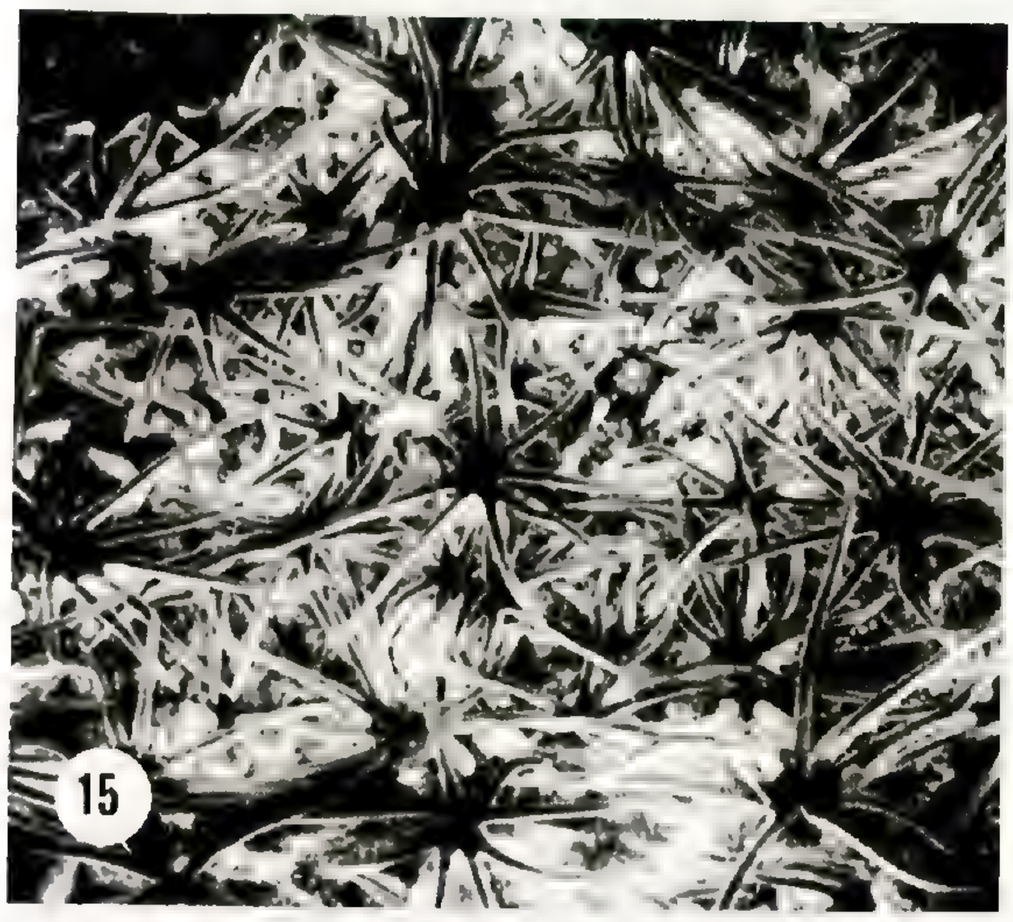
Quercus prinoides Willdenow

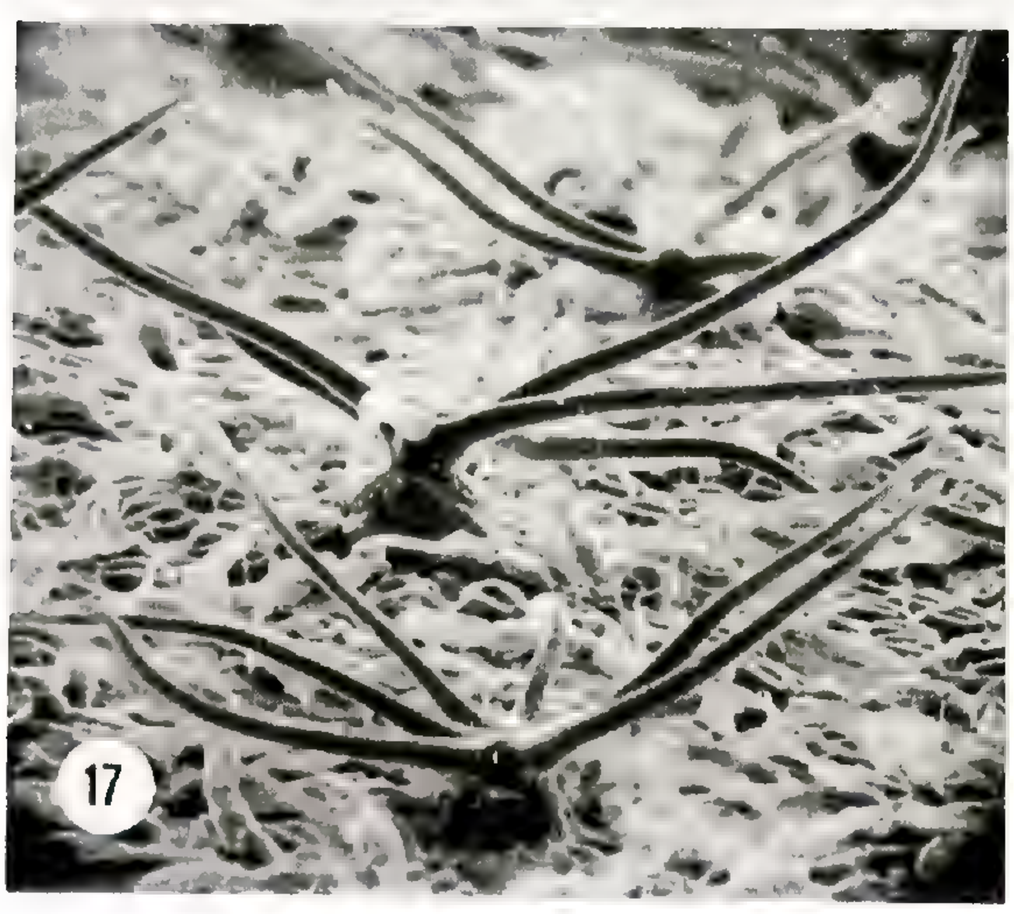
We include in this description both var. *prinoides*, the dwarf chinquapin oak, and the chinquapin oak, var. *acuminata* (Michaux) Gleason (*Quercus muehlenbergii* Engelm. of many authors), electing to follow Gleason in considering them varieties of *Q. prinoides* (FIGURE 15).

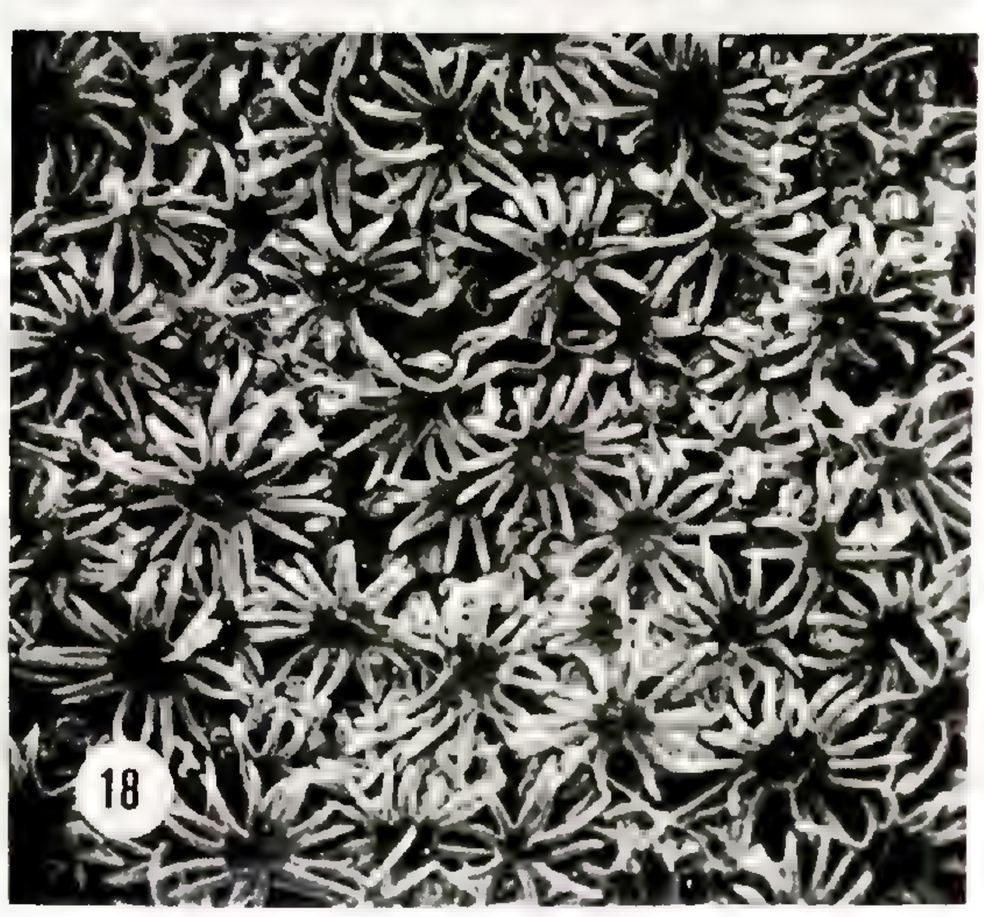
Var. prinoides

Trichomes of the dwarf chinquapin oak are stellate, appressed or looser, and whitened or with a yellowish tint; they occur on the leaf surface and lateral surfaces of the midvein and primary veins, but are conspicuously absent from the ventral surface. The hairs are small, 0.09–0.22 mm. ($\overline{X}$

= 0.15 mm.) across, and have 6 to 16 rays per trichome ($\overline{X}$ = 10.2). Glandular hairs may or may not be present.







FIGURES 13–18: 13, *Quercus montana*, stipitate-fasciculate hairs (vein axils) and fasciculate hairs (lamina surface), × 50; 14, *Q. oglethorpensis*, stipitate-fasciculate hairs, × 150; 15, *Q. prinoides*, stellate hairs, × 250; 16, *Q. prinus* solitary and fasciculate hairs, × 150; 17, *Q. stellata*, fasciculate hairs, × 250 18, *Q. virginiana*, sessile, fused-stellate hairs, × 200.

Var. **acuminata** (Michaux) Gleason

Chinquapin oak trichomes do not differ in type, occurrence, color, or significantly in ray number (6 to 16, ($\overline{X}$ = 9.2) or spread (0.09–0.22 mm. ($\overline{X}$ = 0.14 mm.) from the dwarf.

Much of the material for this species was taken from field populations, but herbarium specimens were also used. In all 22 populations, a relationship to *Quercus macrocarpa* is seen in some individuals that possess a fasciculate trichome conforming in range and average for quantitative characters to the fasciculate hairs on burr oak. The smaller, stellate hairs of burr oak are nearly identical to those of *Q. prinoides* (TABLE 1). The wide leaf form of var. *acuminata* (f. *alexanderi* (Britton) Steyermark) frequently has only the larger trichomes, a condition sometimes observed in *Q. macrocarpa*.

Quercus prinus Linnaeus (*Quercus michauxii* Nuttall)

Swamp chestnut oak has the longest trichomes of all the eastern oaks. Without the aid of a microscope or hand lens, they can easily be seen arising laterally from the midvein. Nonglandular hairs are of two types: fasciculate, ranging from 0.20 to 0.45 mm. ($\overline{X}$ = 0.33 mm.) in spread, or solitary. Hairs of both types often exceed 1.0 mm. in length. The hairs are yellow or white with 2 to 4 (to 8) rays ($\overline{X}$ = 3.4). These are associated with bulbous, glandular hairs which may be erect or appressed and reddish brown. The latter occur on the leaf surface (FIGURE 16).

Quercus stellata Wangenheim

As indicated by the specific epithet, trichomes of post oak are indeed stellate in appearance. They occur on pedestals and have a spread of 0.15–0.49 mm. ($\overline{X}$ = 0.31 mm.); the rays range from 4 to 9 ($\overline{X}$ = 6.6). The yellow hairs are distributed upon the midvein and primary veins and are typically associated with small, appressed, glandular ones that are also yellow (FIGURE 17). Although the hairs diverge in nearly the same plane, they are best viewed as fasciculate types since they do show some fusion at the base.

Quercus virginiana Miller

In his 1971 treatment of the Fagaceae, Elias lists three varieties of live oak: var. *virginiana* Small, var. *fusiformis* (Small) Sargent, and var. *maritima* (Michaux) Sargent. We have treated var. *maritima* as *Q. geminata* and have discussed it separately. Described here are vars. *virginiana* and *fusiformis*. FIGURE 18 shows trichomes of *Quercus virginiana*.

Var. **virginiana**

This variety, along with var. *fusiformis* and *Quercus minima* (treated by some as *Quercus virginiana* var. *minima* Sargent), is unique in the structure of its nonglandular trichomes. The hairs are fused-stellate, appressed, and quite small. Spread varies from 0.06 to 0.18 mm. ($\overline{X}$ = 0.11 mm.).

Despite their small size, the rays are numerous. Counts ranged from 9 to 18, with 15.6 the average.

Var. **fusiformis** (Small) Sargent

Trichomes differ slightly from var. *virginiana*. Rays range from 12 to 24 ($\mathbf{X}$ = 17.1) but have about the same spread, 0.08–0.16 mm. ($\bar{\mathbf{X}}$ = 0.12 mm.). This variety was observed to possess yellow, appressed, glandular hairs that are typically absent in var. *virginiana*.

DISCUSSION AND CONCLUSIONS

The trichome types that offer the greatest utility for taxonomic studies of species of white oaks are nonglandular. From TABLE 1 it is evident that the fasciculate type is more prevalent than the others. When nonglandular trichomes of all types are considered, those trichomes with an even number of branches are more common than those with an odd number, and hairs with eight branches are most frequent. Glandular hairs do not lend themselves as readily for taxonomic work but are important on the basis of their presence or absence.

If their qualitative and quantitative features are combined, foliar trichomes of the eastern white oaks are separable into combinations that can be associated with established species. For a given species, variation may occur in the quantitative aspects of trichome structure over its geographic range (and probably also over its ecological amplitude), but the types present are quite uniform. For example, the fasciculate and stellate nonglandular hairs plus the red, bulbous, glandular ones provide a unique combination that is seen on leaves of *Quercus bicolor* from New York to Missouri. Spread, number of rays, and density, however, do vary within established limits, but the combination holds throughout the range. In this regard, trichomes are stable characters, perhaps more so than other qualitative features such as leaf shape.

Once the basic patterns are recognized, trichomes may be employed, with the aid of a hand lens, as useful characters in diagnostic keys for use in the field. Indeed, a key based on vegetative features in light of this evidence is planned for the eastern white oaks. Although mature leaves were used in developing the trichome descriptions, some seedlings and a few specimens with immature foliage were seen. At this time insufficient material has been examined for us to state with certainty that trichome evidence is applicable to their determination, but what we have observed encourages us to make the necessary collections in the coming year.

Trichome evidence is certainly of significance in systematic studies of the oaks and, as indicated above, has been used in combination with other characters by some investigators to establish parentage of putative hybrids. During the summer of 1974, we collected a specimen from an individual occurring in western Missouri that we suspected from leaf and fruit morphology might be a hybrid involving *Quercus stellata* and *Q. macrocarpa* (= *Q.* × *guadalupensis* Sargent). Examination of the leaves of

this individual showed it to possess nonglandular hairs of two sizes as well as glandular ones. The larger nonglandular trichomes are fasciculate and are mounted on pedestals. Their ascending rays average 6.5 per trichome and have a mean spread of 0.51 mm. The smaller nonglandular hairs are stellate with an average of 7.8 rays and a mean spread of 0.15 mm. In being attached to pedestals and having an average of 6.5 rays per hair, the fasciculate trichome resembles that of *Q. stellata*. However, the hairs are similar to those of *Q. macrocarpa* in spread and divergence. We believe the combinations of characters in these fasciculate hairs offer evidence of hybridization between the two species (FIGURE 19).

Interestingly, the stellate hairs of the suspected hybrid do not differ from those of *Quercus macrocarpa*. It is speculative at this point, but perhaps genes controlling production of different hair types are on different chromosomes, and the stellate hairs of *Q. macrocarpa* have been passed unmodified to the hybrid offspring.

The utility of trichome evidence in hybridization studies is not restricted to the eastern oaks. In a preliminary statement regarding a complex series of hybridizations among seven species of western white oaks, Tucker (1960) proposed that (among others) *Quercus gambelii* and *Q. grisea* had each crossed with *Q. muehlenbergii* (*Q. prinoides* var. *acuminata* of this

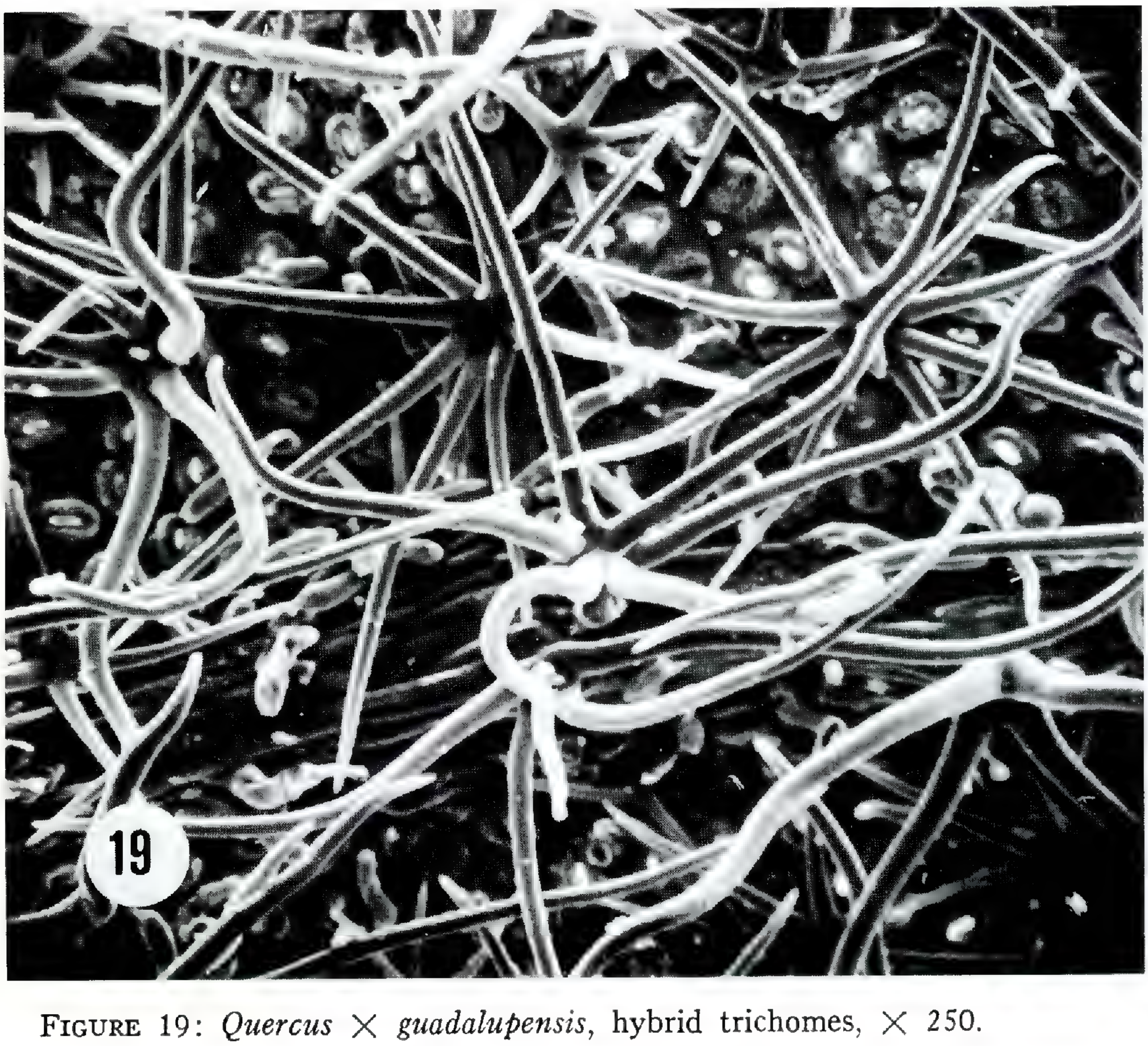


FIGURE 19: *Quercus* × *guadalupensis*, hybrid trichomes, × 250.

study). Evidence in support of these matings has not been presented by Tucker, but hybridizations involving *Q. prinoides* have been the subject of a separate study by Thomson (1978).

Plants believed to represent the crosses suggested by Tucker, and their putative parents, were collected in the Capitan Mountains of New Mexico during the summer of 1976. In both matings trichome evidence is of importance in establishing identity of the supposed parental taxa.

Quercus gambelii has nonglandular trichomes with four or fewer rays (FIGURE 20). The stellate trichomes of *Q. prinoides* (FIGURE 24) typically have eight or more rays. Both trichome types are present on leaves of *Q. gambelii* × *Q. prinoides* (FIGURE 22). *Quercus grisea* possesses nonglandular trichomes with contorted rays (FIGURE 21). The hybrid *Q. grisea* × *Q. prinoides* bears trichome types of both parents (FIGURE 23).

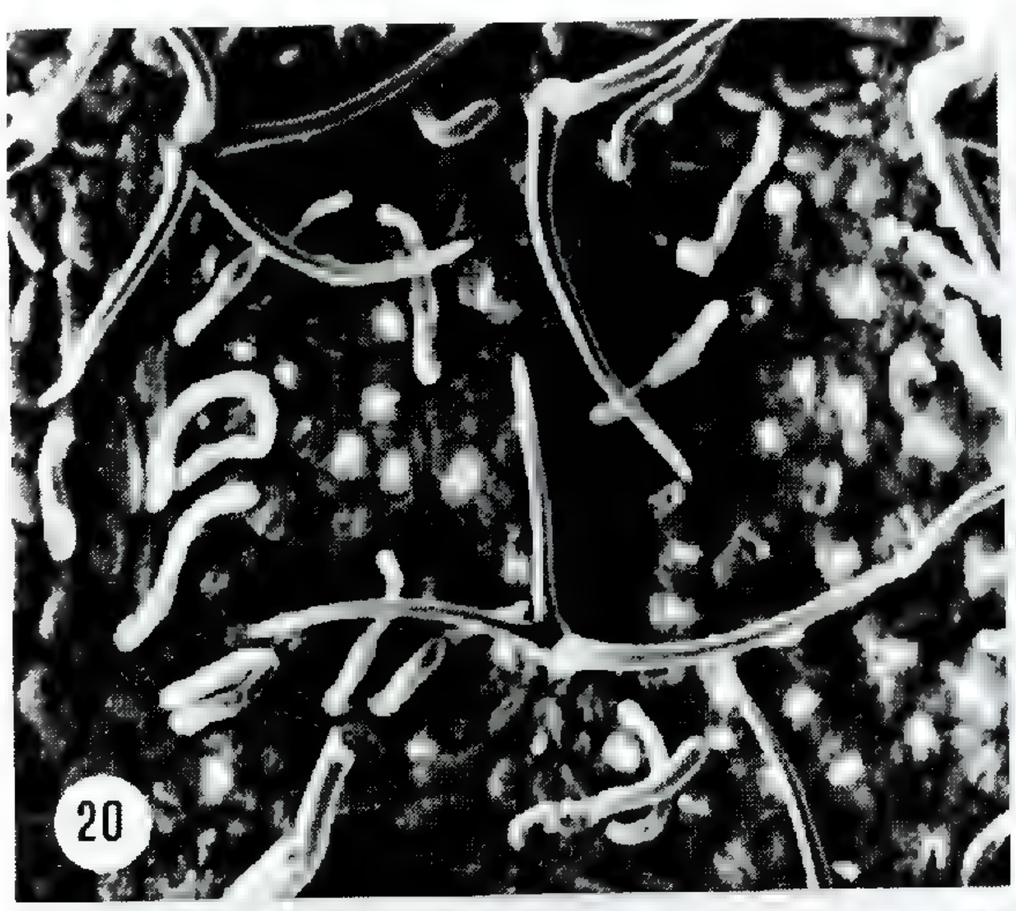
In the three examples of hybridization presented here, trichomes seem to be inherited in one of two basic ways. If the parent species have one or more trichomes of the same type (e.g., fasciculate hairs occur on the parents of *Quercus* × *guadalupensis*), hybrids demonstrate intermediacy in the quantitative features of spread and number of rays. In the second case, if parental species have trichomes of different types (e.g., fasciculate for *Q. grisea* and stellate for *Q. prinoides*), then the hybrids possess both types of hairs. In either event the trichome pattern typical of the parents is altered by the hybridization. Because the types of trichomes, their spread, and the number of rays per hair are so uniform for a species, modifications such as those described above provide strong evidence for hybridization.

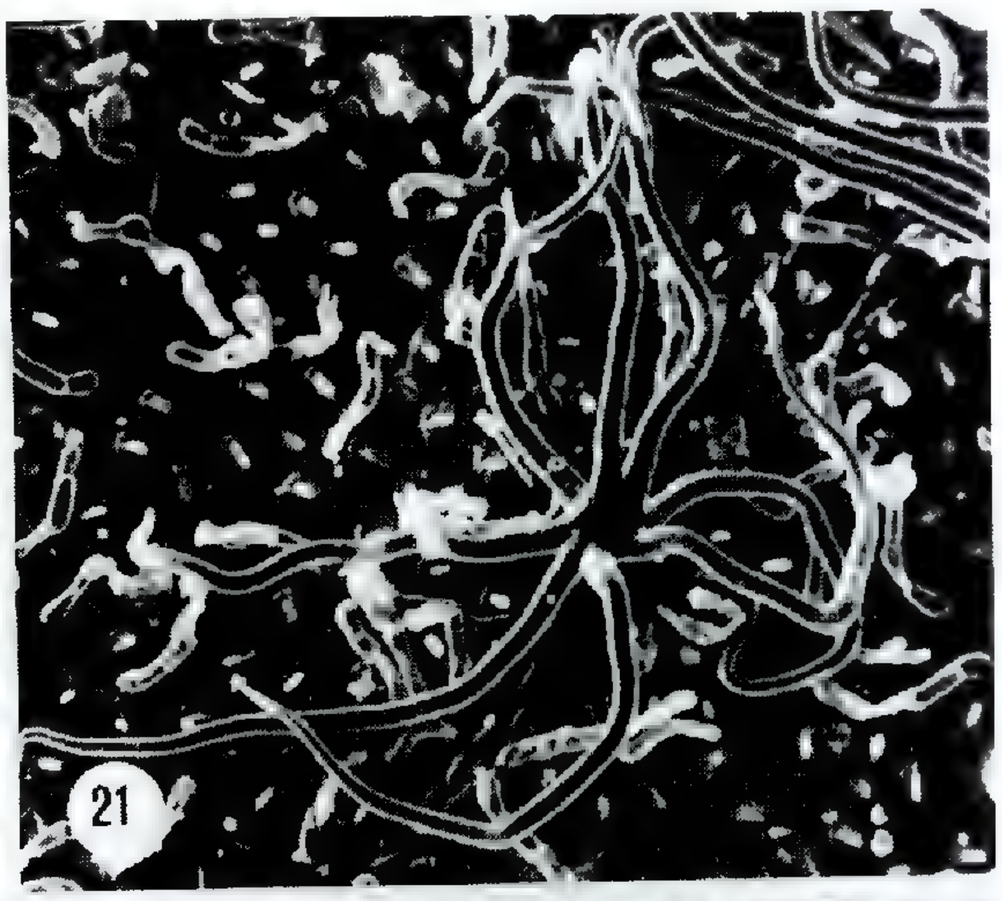
That trichome evidence may be useful in formulating phylogenetic series may be seen in its application to a lineage proposed by Duncan (1950). His phylogenetic tree for eight oaks included *Quercus oglethorpensis*, *Q. margaretta*, *Q. stellata*, and *Q. chapmanii* on one branch, and *Q. breviloba*, *Q. durandii*, *Q. austrina*, and *Q. alba* on the other. With respect to the first series, we think it is more than coincidental that trichomes of the four species are attached to pedestals, are fasciculate, have rays which vary from 4 to 9, have a mode of 8, and average 6.3, 6.7, 6.6, and 6.8, respectively. They differ in spread, decreasing nearly in accordance with the series suggested.

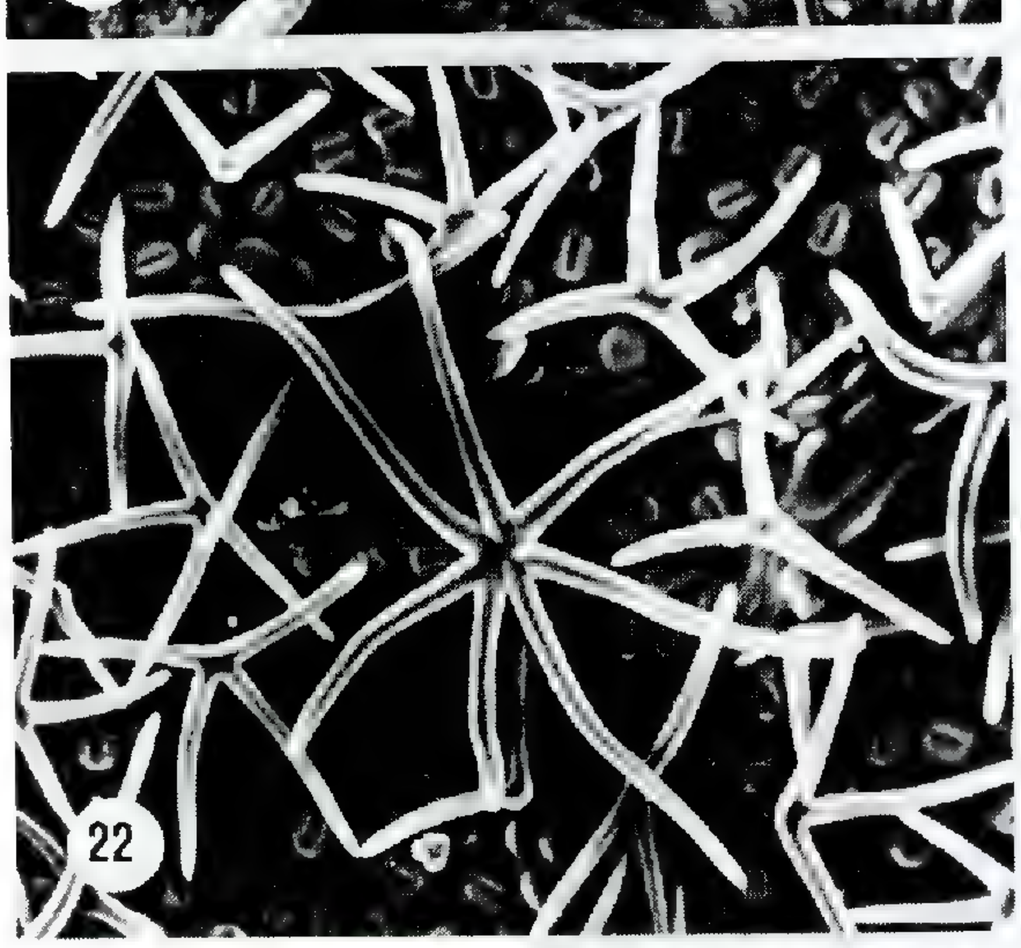
Hardin (1976) speculated that evolutionary modifications within the nonglandular class of trichomes progressed from single- to multi-celled hairs and toward vertical fusion for fascicular types. Duncan's series, which relates primitiveness to geologic distribution, portrays the phylogenetic sequence in reverse order with respect to trends in trichome structure. In his scheme *Quercus oglethorpensis* is the most primitive, but its trichomes are the advanced, stipitate-fasciculate type and lack any unicellular hairs. The most advanced, *Q. chapmanii*, has less specialized nonglandular trichomes along with simple-uniseriate ones. If fusion followed nonfused forms in the oaks, then the trends in Duncan's series are secondary.

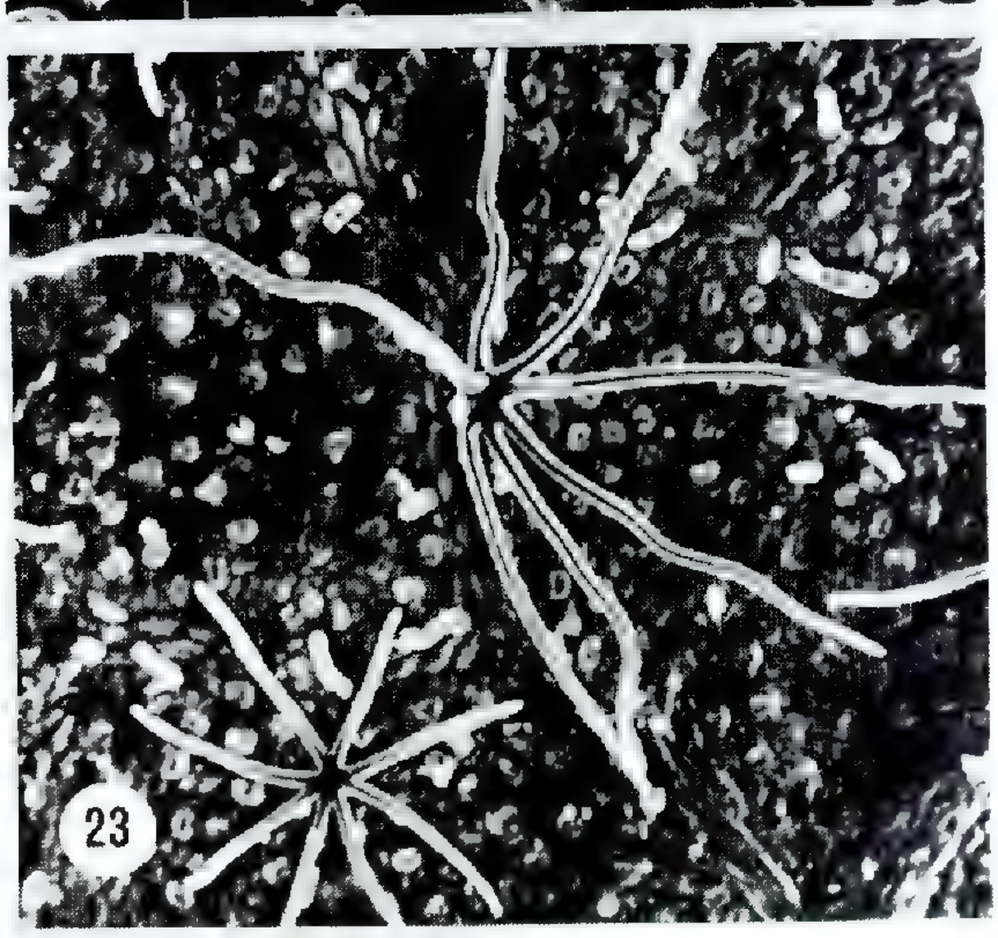
In a study of the live oak group, Muller (1963) stated that *Quercus virginiana* occurs on soils of very recent formation. It is interesting that

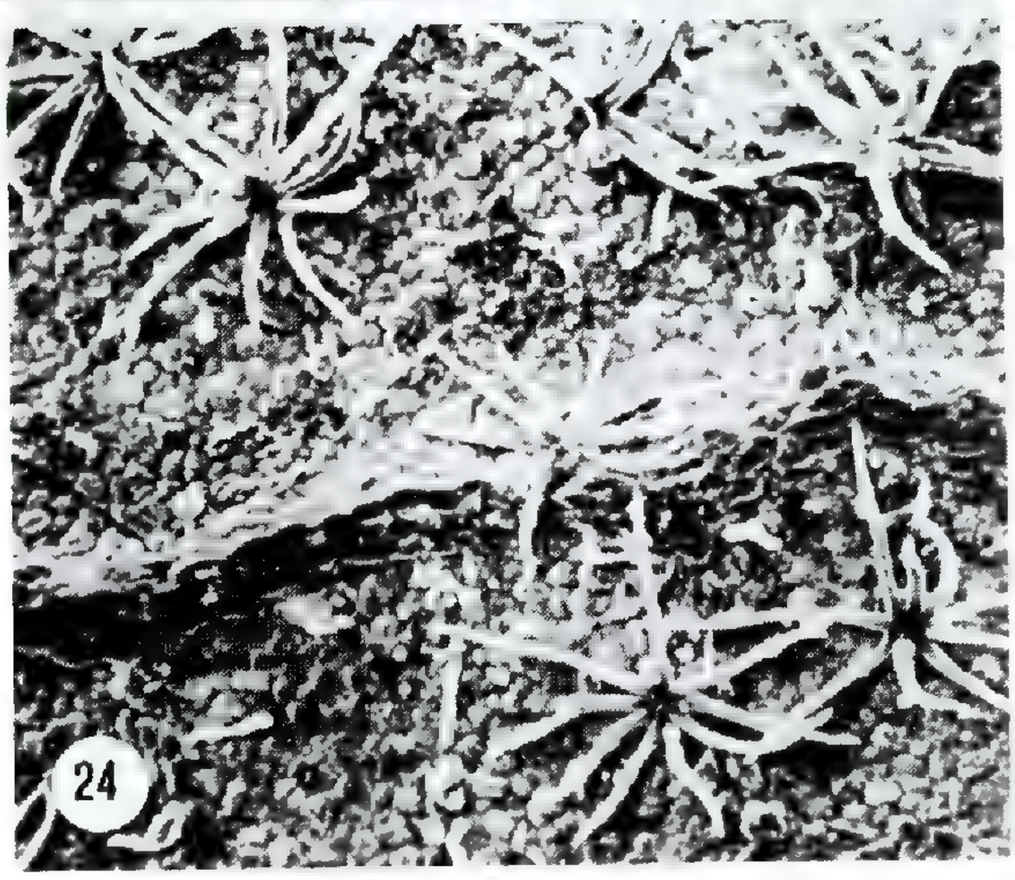
this species has one of the most advanced trichome structures, the fused-stellate type. It seems to us that trichome evidence, when combined with geologic age of the substratum, will prove to be a useful aid in interpreting phylogenetic series in this group. However, as with most morphological











FIGURES 20–24: 20, *Quercus gambelii*, fasciculate hairs, × 220; 21, *Q. grisea*, fasciculate hair, × 130; 22, *Q. gambelii* × *Q. prinoides*, hybrid trichomes, × 220; 23, *Q. grisea* × *Q. prinoides*, hybrid trichomes, × 130; 24, *Q. prinoides*, stellate hairs, × 130.

characters, without time references it is not possible to indicate for a group whether specializations are primitively simple or simple by reduction.

ACKNOWLEDGMENTS

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CERCIDIPHYLLACEAE HARDY IN TEMPERATE NORTH AMERICA[1]

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CERCIDIPHYLLACEAE Engler, Syllabus Pflanzenfam. ed. 6. 132. 1909, nom. cons.

(CERCIDIPHYLLUM FAMILY)

A small, isolated family of dioecious trees producing long and short shoots with stipulate, dimorphic leaves exhibiting either palmate or nearly palmate venation, the short shoots producing solitary leaves and ultimately staminate or carpellate inflorescences; staminate inflorescences comprising several apetalous flowers, each consisting of a fascicle of numerous stamens subtended by a membranous bract; carpellate inflorescences of (2? or) 3–7 apetalous flowers, each consisting of a unilocular carpel subtended by a membranous bract. Fruit a follicle dehiscent along its abaxial suture, the numerous seeds winged at one or both ends. TYPE GENUS: *Cercidiphyllum* Siebold & Zuccarini.

A unigeneric family of eastern Asia in China and Japan. The genus *Cercidiphyllum* was initially included in the Magnoliaceae, but anatomical, palynological, and especially morphological evidence suggest that the Cercidiphyllaceae, along with the Trochodendraceae, Tetracentraceae, Eupteleaceae, and Eucommiaceae, other anomolous families with which it has been grouped, should be excluded from the magnoliaceous assemblage and aligned with the hamamelidaceous lineage, where they are more easily accomodated. Recent schemes of classification proposed by Thorne (1968, 1976), Takhtajan (1969), and Cronquist (1968) are in general agreement

[1] This treatment of the Cercidiphyllaceae is the sixth contribution in a series of treatments of cultivated ligneous plants, the preparation of which is a project of the Arnold Arboretum of Harvard University, and the purpose of which is to provide a modern, accurate account of the woody plants encountered in cultivation in the cooler temperate regions of North America. It is hoped that these studies will eventually form the basis for a new manual of cultivated woody plants. The first paper in the series was published in the Journal of the Arnold Arboretum **56**: 1–19. 1975. Reference should be made to the introductory paragraphs of that paper for matters concerning area covered, taxa included, and the general philosophy of these treatments.

Special thanks and gratitude are extended to the Director and trustees of the Stanley Smith Horticultural Trust for a grant that has made possible the illustrations that accompany this treatment. The illustrations are the careful work of Robin S. Lefberg and were prepared from living and alcohol-preserved specimens growing in and collected at the Arnold Arboretum and dried specimens in the herbaria of the Arnold Arboretum and Gray Herbarium. I extend my appreciation to Dr. S. Y. Hu for translations from the Chinese, to F. Vrugtman for specimens from the Royal Botanical Garden, Hamilton, Ontario, and to Dr. P. F. Stevens for helpful discussions.

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on this, although they differ in detail. The family Cercidiphyllaceae is nevertheless an isolated one, with no close relatives in the extant angiosperm flora. In cultivation *Cercidiphyllum* is highly valued as an ornamental shade tree and a botanical curiosity.

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Cercidiphyllum Siebold & Zuccarini, Abh. Math.-Phys. Cl. Akad. Wiss. München 4(3): 238. 1846; Fl. Jap. Fam. Nat. 2: 114. 1846.

Large, deciduous trees of sympodial growth; after a juvenile stage of long shoot growth the shoots becoming differentiated into long and short shoots, the long shoots with a small, inconspicuous pith; winter buds with 2 imbricated outer scales and 1 inner scale, the outermost scale adaxial, the buds produced on long shoots giving rise to short shoots in the second year of growth, and subsequent long shoots developed from short shoots. Leaves petiolate, involute in bud with well-developed marginal glands, stipulate, the stipules caducous or persistent, free or connate and adnate to the base of the adaxial surface of the petiole; long shoot leaves opposite and/or subopposite to alternate, with rounded to truncate bases and palmate to nearly palmate venation, those of short shoots solitary, with shallowly to deeply cordate bases and palmate venation. Flowers appearing in spring prior to and/or with the leaves in terminal, apparently greatly reduced and condensed racemes (*fide* Swamy & Bailey) from short shoots. Staminate inflorescences subsessile, consisting of numerous (upwards of 40) stamens, these aggregated into ± distinct groups (flowers), each group ± subtended by an erose, membranous bract; perianth absent; anther filaments at first short, elongating during anthesis; anthers reddish, basifixed, linear-oblong with conical to somewhat acute apices, 2-locular, dehiscent by longitudinal slits; pollen 3-colpate or 3-colpoidate, typically 3-lobate. Carpellate inflorescences pedunculate, the (2? or) 3–7 carpels (flowers) shortly stipitate, inserted at or toward the distal end of the peduncle, each subtended by an erose, membranous bract; perianth absent; carpels ± cylindrical, constricted above and produced into a long slender style with 2 decurrent stigmatic ridges, these often appearing as one; ovaries unilocular with numerous anatropous, bitegmic, crassinucellar ovules on 2 parietal placentae adjacent to the abaxial suture. Fruits ± woody follicles clustered together on the peduncle and dehiscent along the abaxial sutures; seeds numerous, small, ± oblong in outline, the testa

winged at one or both ends; embryo small, embedded in *ab initio* Cellular endosperm, the embryo sac of the Polygonum type; embryogeny corresponding to the Caryophyllad type. TYPE SPECIES: *C. japonicum* Siebold & Zuccarini ex J. Hoffmann & Schultes. (Name from *Cercis* and Greek *phyllon*, leaf, in reference to the similarity of the leaves of short shoots to those of the redbud or Judas tree, *Cercis siliquastrum* L.) — KATSURA.

Two extant species of China and Japan; once widely distributed throughout the North Temperate Zone in Eurasia and North America and represented in the fossil record from the Late Cretaceous to the Pliocene by five described form species, of which one corresponds closely to the extant *Cercidiphyllum japonicum*.

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KEY TO THE SPECIES OF CERCIDIPHYLLUM

1. Plants with the short shoots weakly developed, to ca. 6 mm. long; stipules of short shoot leaves long, caducous; stipules of long shoot leaves free or basally connate; follicles with ± straight to slightly recurved apices; seeds winged at the proximal end. ..... 1. *C. japonicum.*
1. Plants with the short shoots strongly developed, to 18 mm. long; stipules of short shoot leaves short, persistent; stipules of long shoot leaves connate; follicles with strongly recurved apices; seeds winged at both ends. ..... 2. *C. magnificum.*

1. **C. japonicum** Siebold & Zuccarini ex J. Hoffmann & Schultes, Jour. Asiatique, IV. **20:** 282. 1852; Noms Indig. Pl. Japon Chine, 26. 1853. FIGURES 1; 2, a–q.

Large trees to 20 or 25 m., occasionally to 35 m., with grayish black or grayish brown, deeply furrowed, and spirally twisted bark even when

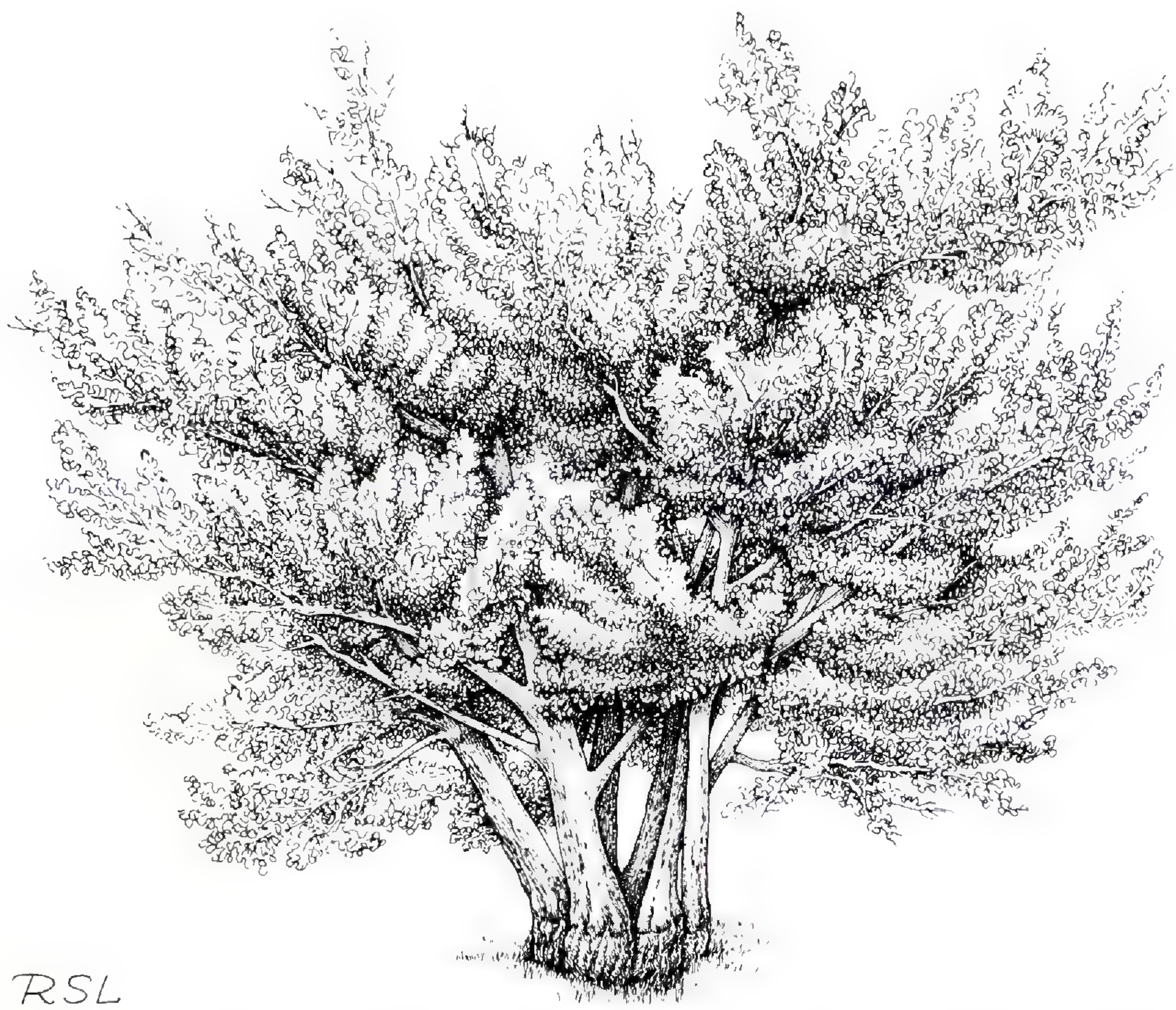

FIGURE 1. **Cercidiphyllum japonicum:** habit drawing of one of the old carpellate trees growing in the Arnold Arboretum. This tree (AA #882-B) was grown from seed received at the Arnold Arboretum on April 29, 1878, that had been collected by Professor W. S. Clark in Hokkaido, Japan. Approximately 100 years old, this specimen is about 10 meters (35 feet) in height and illustrates the multiple trunks developed by many individuals of the species.

young, the plants often ± fastigiate when small, sometimes with a single trunk or often with several trunks diverging from or near the base; short shoots poorly developed, to ca. 6 mm. long; long shoots lenticellate, reddish brown, becoming silvery or grayish, the periderm exfoliating in thin sheets, the terminal portion of the current year's growth dying back and deciduous, resulting in a solitary or usually 2 opposite to subopposite pseudoterminal buds; winter buds 4–5 mm. long, acute, reddish, the outermost scale overlapping the 2 inner ones. Leaves initially reddish, becoming green or bluish green, turning yellow to pastel pink (or scarlet?) in fall, solitary on short shoots, opposite to alternate on long shoots. Long shoot leaves petiolate and stipulate, the petioles (1.3–)1.5–2 cm. long, the stipules free or basally connate, 8–9 mm. long, ± filiform, membranous, shriveling after the blade has expanded; leaf blades 3.2–4.5 cm. long, 1.9–3.2(–3.8) cm. wide, ovate, elliptic, or slightly obovate, with rounded, truncate, or broadly cuneate bases and crenate to serrulate margins, the venation palmate to pinnate. Short shoot leaves petiolate and stipulate, the petioles 1.4–4.7 cm. long, the stipules connate, 5–6 mm. long, membranous, ± lanceolate with laciniate, bifid or trifid apices, caducous and evident only as the leaf expands from the bud in spring; leaf blades glabrous, (3.3–)3.7–9 cm. long, (3.7–)5–8.3(–9.2) cm. wide, broadly ovate to reniform with shallowly to deeply cordate bases and crenate margins, the venation palmate; lower surfaces of the blades occasionally ± glaucous. Inflorescences at anthesis protruding from the opening buds; staminate inflorescences consisting of numerous (20–40) stamens, the anthers ca. 5 mm. long, reddish- to pinkish-tinged, borne on slender, white filaments, these elongating at anthesis; carpellate inflorescences consisting of 3–7 carpels inserted at or near the apex of a short peduncle 3–5 mm. long, each subtended by an erose bract to 3 mm. long, the greenish ovaries ca. 3 mm. long, sessile to shortly stipitate, the styles to 14 mm. long, twisted and often curved or hooked toward the apex, the decurrent stigmas reddish to pinkish, shriveling after anthesis. Follicles initially green, becoming purplish brown, ± glaucous and woody, 1.4–1.8 cm. long, cylindrical, slightly recurved at the apex and often with a short stylar beak before dehiscence, held ± erect and widely dehiscent along the abaxial suture at maturity, then with rounded to retuse apices and usually persistent into the following growing season; seeds numerous, small, 4–5 mm. long, closely imbricated, ± pendulous, in 2 rows, the seed coat tan, the embryo at the proximal end, the testa forming a small, ± oblong proximal wing. $2n = 38$. (Including *C. ovale* Maximowicz.) — KATSURA, KATSURA-TREE.

Widely distributed in mountainous areas throughout the Japanese islands of Honshu, Shikoku, and Kyushu but most common in northern Honshu and in central and western Hokkaido, where it occurs near sea level (see distribution map, p. 277, in Kurata, 1971); also known in China in Hupeh, Szechwan, and Shensi provinces (see below), and widely cultivated in North America. In Japan, where it grows in deep, rich soils, *Cercidiphyllum japonicum* is an important forest tree valued for its light, soft

wood that is utilized in cabinetry work and for the interior finish of buildings.

Plants with the lower surfaces of the short shoot leaves ± sericeous along the veins toward the base and with puberulent follicles have been recognized as *Cercidiphyllum japonicum* f. *miquelianum* Inokuma, Bull. Tokyo Imp. Univ. Forests **25**: 29. 1937 (*C. japonicum* var. *sinense* Rehder & Wilson, Pl. Wilsonianae 1: 316. 1913). This form occurs sporadically in Japan and China. Judged on the basis of herbarium specimens at A and GH, it is the most commonly collected *Cercidiphyllum* from China, occurring in Szechwan, Anhwei, and Hupeh provinces. Chinese botanists (Anonymous, 1972) record *C. japonicum* (as var. *sinense*) from the provinces listed above as well as from Shansi, Shensi, Honan, Kansu, Chekiang, and Kiangsi, but I do not know to which forms plants from these latter provinces correspond. Following Rehder and Wilson, most authors have referred specimens of *Cercidiphyllum* from China to *C. japonicum* var. *sinense*, yet some Chinese specimens, including a few cited by Rehder and Wilson in the protologue of var. *sinense*, are completely glabrous and conform to f. *japonicum*. These glabrous plants occur (based on herbarium records) in the provinces listed under the distribution given for the species.

Except for the pubescence of the leaves and follicles, plants of *Cercidiphyllum japonicum* f. *miquelianum* do not differ from typical *C. japonicum*. While Rehder and Wilson further distinguished between the two taxa on the basis of growth habit (the pubescent-leaved plants usually with a single trunk, the glabrous-leaved plants most commonly with several trunks from near or at the base), this distinction, due to exceptions and intergradations, does not appear to be of taxonomic significance. As a result, I consider that recognition of the pubescent-leaved plants is more appropriate as a form, and Inokuma's name, based on a Japanese plant, is available in that rank.

Concerning *Cercidiphyllum* in China, Wilson (in Rehder & Wilson, 1913, p. 317) noted "both in height and girth this tree exceeds all other broad-leaved deciduous trees known. . . ." Chinese botanists (Anonymous, 1972) record that an extract made from its bark and leaves is used as a glue or birdlime.

2. **C. magnificum** (Nakai) Nakai, Cat. Sem. Spor., Hort. Bot. Univ. Imp. Tokyo. 35. 1920. FIGURE 2, r–t.

Forest trees, similar in morphology and growth to *Cercidiphyllum japonicum* but differing in several significant respects; the trees with but a single bole (*fide* Lindquist); the bark remaining smooth, becoming furrowed only at an advanced age; short shoots strongly developed, to ca. 18 mm. long. Long shoot leaves petiolate and stipulate, the petioles 1–2.6 cm. long, the stipules connate, ± oblong to widely ovate with a bifid apex, ca. 1 mm. long, persistent; leaf blades longer than wide, (2.7–)5–8.3 cm. long, (2–)3–5.8 cm. wide, ovate to elliptic with truncate, rounded, or broadly cuneate bases. Short shoot leaves petiolate and stipulate, the petioles (1.2–)1.7–3.2 cm. long, the stipules connate, ca. 3 mm. long, membranous, ± broadly ovate with a bifid or trifid apex, persistent and evident at the base

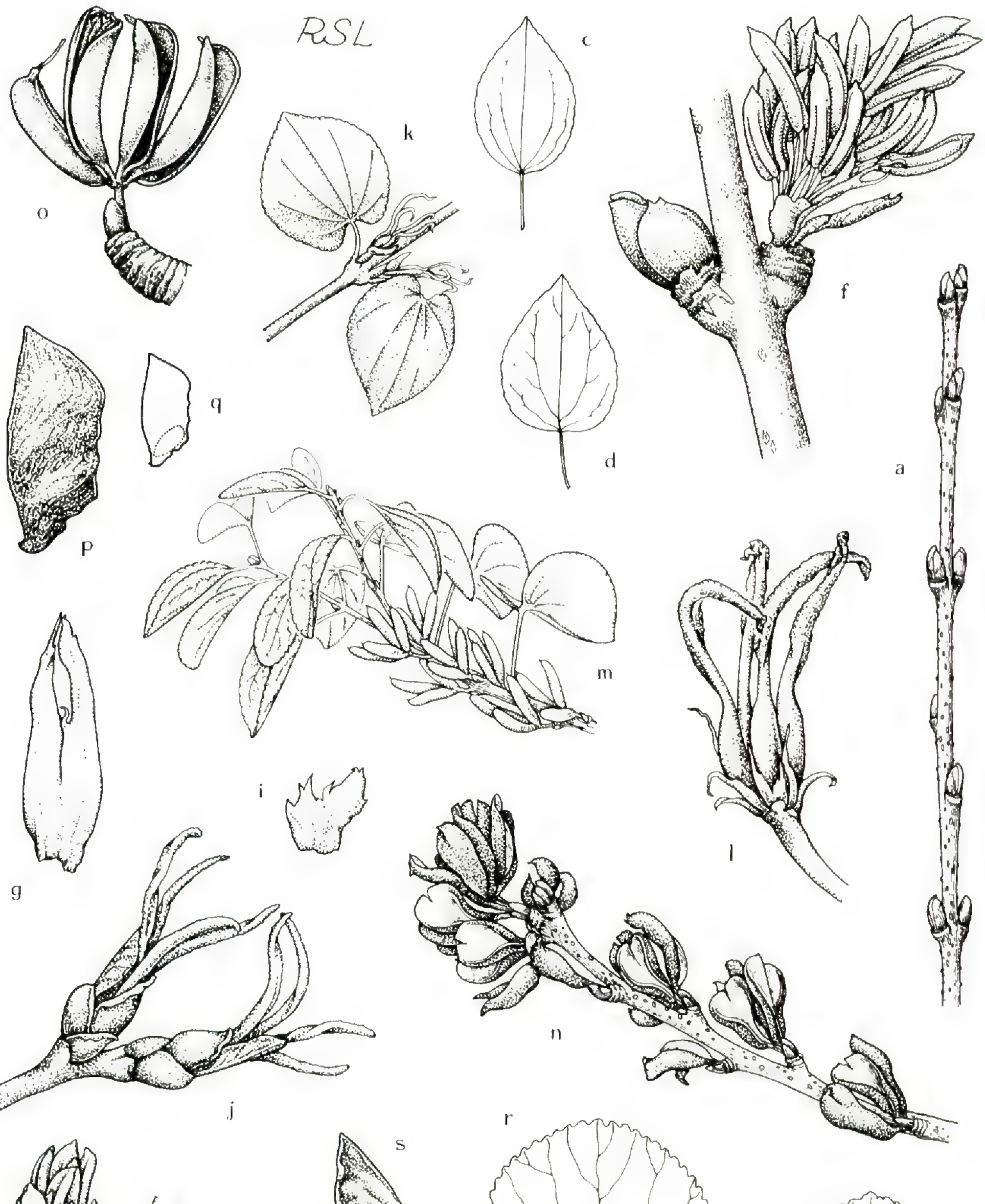

FIGURE 2. **Cercidiphyllum.** a–q, *C. japonicum*: a, portion of long shoot of previous year's growth with dormant winter buds, × 1; b, outline of typical short shoot leaf, showing palmate venation, × ½; c, d, outline of typical long

of the petiole throughout the growing season; leaf blades glabrous, (3–)4–7(–8.5) cm. long, (2.5–)3.4–7.7(–9.6) cm. wide, broadly ovate, rotund, or reniform, with cordate bases, in herbarium specimens the lobes often overlapping the petiole at the point of its insertion. Inflorescences produced from short shoots in early spring, apparently very similar to those of *C. japonicum*.[2] Follicles 2–6, clustered together on short peduncles 5–6 mm. long, the peduncles often persistent on the short shoots 2 or 3 years after the follicles have fallen; follicles purplish brown to pinkish, faintly to strongly glaucous, 1.2–2 cm. long, cylindrical, strongly recurved toward the apex and often with a stylar beak, at maturity dehiscing only slightly from the apex along the abaxial suture; seeds numerous, small, ca. 6 mm. long, the seed coat creamy tan, the embryo centrally situated, the testa forming small wings at both the distal and proximal ends. $2n = 38$. (*C. japonicum* Sieb. & Zucc. ex J. Hoffm. & Schultes var. *magnificum* Nakai, Bot. Mag. Tokyo 33: 198. 1919; *ibid.* 299. (In Japanese).)

Endemic to Japan on the island of Honshu, where data from herbarium specimens at A and GH indicate its occurrence in Iwate (Mt. Hayachine), Tochigi, Nagano, and Gifu prefectures. Lindquist's (1954) distribution map, showing that *Cercidiphyllum magnificum* is largely confined to the Japanese alps and the Nikko region, essentially coincides with this information. *Cercidiphyllum magnificum* appears to occur in regions where *C. japonicum* is either absent or rare, and Ohwi (1965) states that *C. magnificum* grows at higher elevations than does *C. japonicum*.

Seeds of *Cercidiphyllum magnificum* were received at the Arnold Arboretum from the University of Tokyo in 1920, but I do not know if these seeds were shared with other American or European botanical gardens and arboreta. Unfortunately, none of the plants grown from that seed lot survives in the Arboretum. Subsequent introductions by other institutions (some, perhaps, also in 1920) have established the species in limited numbers in western gardens.

[2] Only three herbarium specimens representing staminate plants in the later stages of flowering have been available for study. Examination of carpellate plants with follicles in early stages of maturation suggest that the female inflorescences might sometimes consist of only two "flowers" or carpels.

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shoot leaves, showing near palmate venation, × ½; e, early stage of staminate inflorescence protruding from short shoot bud, × 3; f, later stage of staminate inflorescence, the bud scales removed to expose leaf, stipule, and membranous bract, × 3; g, connate stipules of short shoot leaf, × 6; h, i, 2 membranous bracts of staminate inflorescence, × 6; j, expanding short shoot buds with protruding carpellate inflorescences, × 3; k, habit of carpellate inflorescences after partial short shoot leaf expansion, × ¾; l, carpellate inflorescence at stage shown in k, × 3; m, habit of branchlet with immature follicles, × ½; n, habit of branchlet with fully dehisced follicles and dormant winter buds, × ¾; o, dehisced follicles from one inflorescence on short shoot, × 2; p, seed, × 6; q, outline of seed showing position (dotted line) of embryo, × 3. r–t, *C. magnificum*: r, outline of typical short shoot leaf, × ⅓; s, seed, × 6; t, outline of seed, showing position (dotted line) of embryo, × 3.

Cercidiphyllum magnificum, while extremely close to *C. japonicum*, can be distinguished by the characters contrasted in the key to species as well as by its larger long shoot leaves, its tendency for the base of the lamina of short shoot leaves to overlap the petiole at its insertion, its strongly recurved, only slightly dehiscent follicles, and its yellowish white seeds. Other, less obvious differences include the bark characters and the tendency for the short shoot leaves of *C. magnificum* to be rounder, with more evenly spaced and prominent crenations.

Plants of *Cercidiphyllum* of pendulous habit with slender, arching and drooping branchlets with the leaves borne on slender petioles 3.4–7 cm. long, the blades 5.5–8 cm. long, 3.6–6.2 cm. wide, ovate to elliptic with rounded, truncate, or broadly cuneate bases and shallowly crenate margins, and the lower surfaces of the blades glaucous, are known in cultivation in Japan and North America. These plants also appear to occur sporadically in the wild in Japan (Mt. Iwayama, Morioka, Iwate Prefecture, *Muroi 4229* (A), and perhaps elsewhere), and the plants have been recognized taxonomically as either a variety or a form of *C. japonicum*. Based on the morphology of the leaves and stipules, however, the plants are referable not to *C. japonicum*, but to *C. magnificum*. The new combination necessitated is made here.[3]

Examination of *Cercidiphyllum magnificum* f. *pendulum* reveals that the plants consist entirely of long shoot growth. As a result, the leaves correspond in morphology to long shoot leaves, although of larger dimensions and with longer petioles, and only the one type of leaf is present on the plants. I do not know if juvenility is ever overcome in these plants through the production of short shoots and the concomitant production of flowers. Observations of cultivated plants would be helpful in resolving this question as well as for comparisons with juvenile plants of *C. magnificum* f. *magnificum*.

The few herbarium specimens of *Cercidiphyllum magnificum* f. *pendulum* examined during this study indicate a natural distribution of the form in Iwate Prefecture in northern Honshu. Both *C. japonicum* and *C. magnificum* f. *magnificum* occur in this prefecture (one of the few areas where they may occur together), and this possible coincidence prompts speculation that *C. magnificum* f. *pendulum* might be an interspecific hybrid between the two extant species of *Cercidiphyllum*.

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[3] **Cercidiphyllum magnificum** (Nakai) Nakai forma **pendulum** (Miyoshi ex Makino & Nemoto) Spongberg, comb. nov. BASIONYM: *Cercidiphyllum japonicum* Sieb. & Zucc. ex J. Hoffm. & Schultes var. *pendulum* Miyoshi ex Makino & Nemoto, Fl. Jap. ed. 2. 307. 1931. *Cercidiphyllum japonicum* f. *pendulum* (Miyoshi ex Makino & Nemoto) Ohwi, Fl. Jap. 510. 1953.

FEATURES OF POLLEN FLOW IN GELSEMIUM SEMPERVIRENS (LOGANIACEAE)

ROBERT ORNDUFF

GELSEMIUM SEMPERVIRENS (L.) Jaume Saint-Hilaire (Loganiaceae) is a woody vine that occurs in forested areas of the southeastern United States and of the mountains of southern Mexico and Guatemala. Its large, yellow, usually sweet-scented flowers are distylous; associated with this distyly is a strong self-incompatibility system that severely restricts intramorph and favors intermorph fertilizations (Ornduff, 1970). The flowers of *G. sempervirens* are among the largest produced by any heterostylous species and are freely visited by diverse small- and large-bodied bees, although the latter are probably largely responsible for pollination (Ornduff, 1970). The classical interpretation of distyly is that it is a morphological mechanism that promotes pollination between long-styled ("pin") and short-styled ("thrum") flowers (Darwin, 1877; and numerous subsequent workers). Recent studies of pollen flow patterns in distylous herbaceous genera such as *Lithospermum caroliniense* (J. F. Gmelin) MacM. (Boraginaceae; Levin, 1968), *Jepsonia heterandra* Eastw. (Saxifragaceae; Ornduff, 1971), *Hypericum aegypticum* L. (Hypericaceae; Ornduff, 1975), *Amsinckia* spp. (Boraginaceae; Ornduff, 1976; Ganders, 1976), *Lythrum* spp. (Lythraceae; Ornduff, 1979a), and *Primula vulgaris* L. (Primulaceae; Ornduff, 1979b) have shown that high levels of intramorph pollination also occur. In most species studied, the origin of the intramorph pollen on stigmas is unknown. It may be of intrafloral or geitonogamous origin and/or it may come from other plants of the same morph. This paper discusses pollen production, pollen removal from anthers, and features of stigmatic pollen loads in *G. sempervirens*; observations suggest that much of the intramorph pollen on its stigmas is of intrafloral origin.

MATERIALS AND METHODS

Four populations of *Gelsemium sempervirens* were studied in March and April, 1975: *8153*,[1] 10 miles south of Moncks Corner, Berkeley County, South Carolina; *8154*, 3 miles south of Cades, Williamsburg County, South Carolina; *8160*, Raleigh-Durham airport, Wake County, North Carolina; and *8161*, Globe Road near the Raleigh-Durham airport, Wake County, North Carolina. Buds and open flowers of the South Carolina plants were vapor-fixed in plastic bottles with an FAA-saturated layer of plaster of paris set into the bottom of each one. Flowers of the North Carolina plants were emasculated in the field immediately prior to anthesis, tagged, removed from the plants four days after emasculation, and, along with intact flowers also collected at the same time, preserved as above. Pollen produc-

[1] Collections from the four populations cited here were made by the author.

tion was estimated by removing anthers from buds, crushing them in 0.4 ml. 3 : 1 lactic acid : glycerol, placing a sample of the suspension on a hemacytometer, and counting the number of pollen grains on the grids. To determine the amount of pollen remaining in anthers, the same method was employed, this time using anthers of open flowers. Stigmatic pollen loads were examined by excising stigmas of open flowers, acetolyzing them, placing the centrifuged acetolyzate in lactic acid/glycerol, shaking the suspension for a standard period of time, placing a sample of the suspension on a hemacytometer, and estimating the total pollen load by counting the number of pollen grains on the grids.

RESULTS

Pollen production of pins in the two populations sampled for this trait exceeds that of thrums by a factor of 1.2 (TABLE 1). Although the average sizes of pin and thrum pollen grains are different, measurements of the two overlap to such a degree that it is impossible to discriminate consistently between the two types of pollen grains in stigmatic pollen loads. The size and composition of pollen loads on stigmas of flowers varied; in three of the four samples the total conspecific pollen load on pin stigmas was larger than that on thrums; in a fourth sample the reverse was true (TABLE 1). Foreign pollen made up from 6 to 22 percent of the stigmatic pollen loads of pins and from 4 to 16 percent of those of thrums. In population *8153*, 45 percent of the pollen produced by pins and 56 percent of that produced by thrums remained in anthers; in population *8154*, the figures were 74 and 24 percent, respectively. Pollen production figures are not available for populations *8160* and *8161*, but in both populations substantial pollen also was present in the anthers of open flowers of both forms. The stigmatic pollen loads of emasculated flowers of population *8160* were all smaller than those of intact flowers; the difference in size of the load was 68 and 64 percent for pin and thrum stigmas of this population, and 63 and 90 percent for pin and thrum stigmas of population *8161*. In three out of four samples, there were more foreign pollen grains on stigmas of emasculated flowers than on those of intact ones.

DISCUSSION

The difference between pollen production and size of the stigmatic pollen loads between pins and thrums is frequently observed in other unrelated heterostylous plants (cf. references cited above). The former is probably related to average size differences between pollen grains of the forms, while the latter may be the result of the easier accessibility of pin stigmas to visiting insects. Although large amounts of pollen remaining in anthers of open flowers is unusual, it has also been observed in the distylous *Primula vulgaris* L. (Ornduff, 1979b) and *Hedyotis caerulea* (L.) Hooker (Ornduff, unpubl.). It seems likely that in both species this results from a combination of relatively low levels of pollinator activity in very early

TABLE 1. Pollen production, composition of stigmatic pollen loads of intact and emasculated flowers, and estimates of pollen remaining in anthers of flowers of Gelsemium sempervirens.

Collection	Average pollen production per flower		Average number of pollen grains per stigma, intact flowers				Average number of pollen grains per flower, emasculated flowers				Average number of pollen grains remaining in anthers	
	PIN	THRUM	PIN		THRUM		PIN		THRUM		PIN	THRUM
			Conspecific pollen	Foreign pollen	Conspecific pollen	Foreign pollen	Conspecific pollen	Foreign pollen	Conspecific pollen	Foreign pollen		
8153	75,511	63,966	1639	103	622	25	—	—	—	—	34,040	35,660
8154	74,059	61,172	1197	103	1861	81	—	—	—	—	54,760	14,954
8160	Not determined		1397	153	1258	139	944	333	796	102	47,260	11,677
8161	Not determined		1456	404	678	129	926	537	611	204	31,320	19,676

spring and perhaps from a feeding preference for nectar over pollen by insects visiting the flowers. The reason for large amounts of uncollected pollen in anthers of *Gelsemium sempervirens* is unclear. Bees are rather conspicuous in populations of this species when it is in flower, but no observations are available on the frequency of their visits to flowers or on other features of their foraging behavior.

The differences in the size of the conspecific pollen loads on the stigmas of intact and emasculated flowers are of particular interest. Three out of four samples of stigmas of emasculated flowers had pollen loads about one-third smaller than those of intact flowers. Since emasculated and intact flowers were both present in the same population at the same time, the total pollen available to the stigmas of the two types of flowers was the same. Consequently, the fact that stigmas of emasculated flowers of both pins and thrums have reduced pollen loads suggests that much of the pollen on the stigmas of intact flowers is of intrafloral origin. That is, a substantial proportion of pollen movement in the population is from anthers to stigmas of the same flower; clearly, any intermorph pollen on stigmas must be of interfloral origin. An alternative explanation is that emasculated flowers are less attractive to pollinators than are intact ones and are therefore visited by insects less often and/or for shorter periods of time. It is unlikely that this explanation is correct, since thrum stigmas of emasculated flowers of population *8161* received only 10 percent less pollen than those of intact flowers; the increased proportion of foreign pollen in the stigmatic pollen loads of emasculated flowers does not support reduced pollinator visitation; and the corollas have UV-absorbing and UV-reflecting zones (Eisner *et al.*, 1973), suggesting that these patterns are important in attracting insect visitors.

Thus, in *Gelsemium sempervirens* it is probable that substantial levels of intrafloral pollen transfer occur. Ganders (1974) has made a similar suggestion that in the distylous herbs *Jepsonia heterandra*, *Lithospermum caroliniense*, and *Lithospermum californicum* Gray there are moderate levels of self-pollination. Mulcahy and Caporello (1970) have arrived at like conclusions for the tristylous *Lythrum salicaria* L. I have also made a number of observations on *Hedyotis caerulea* that suggest high levels of intrafloral pollen transfer. At first glance, analyses of the composition of stigmatic loads of several heterostylous genera do not strongly support the Darwinian hypothesis concerning the adaptive significance of floral heteromorphism. However, when the interfloral component of stigmatic pollen loads can be distinguished from the intrafloral pollen, heterostyly seems to have a positive effect on intermorph pollen flow.

ACKNOWLEDGMENTS

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HETEROSTYLY IN OPLONIA (ACANTHACEAE)

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IN A RECENT REVIEW of the distribution of heterostyly in flowering plants (Vuilleumier, 1967), the Acanthaceae were not mentioned. Subsequently, however, Stearn (1971) reported distyly for several species of *Oplonia* (FIGURE 1), a shrubby genus of the West Indies, northern South America, and Madagascar, and concluded that "heterostylous floral dimorphism probably occurs throughout the genus." His descriptions of floral morphology indicate that at least eight of the fourteen species exhibit distyly. In view of this apparently unique occurrence of heterostyly in the Acanthaceae, and because of the absence of any information on morphological and physiological traits associated with dimorphism in style length and anther position, I visited Jamaica in 1973, obtained living material of *Oplonia* species, and made field observations on population composition. Subsequently, plants were established at the Botanical Garden of the University of California, Berkeley. These were utilized in the present study, which presents the results of pollen measurements and a crossing program.

MATERIALS AND METHODS

Population composition of two species was determined in the field by recording the floral morphology of all individuals encountered. Pollen size was determined by mounting living pollen in aniline blue-lactophenol on a

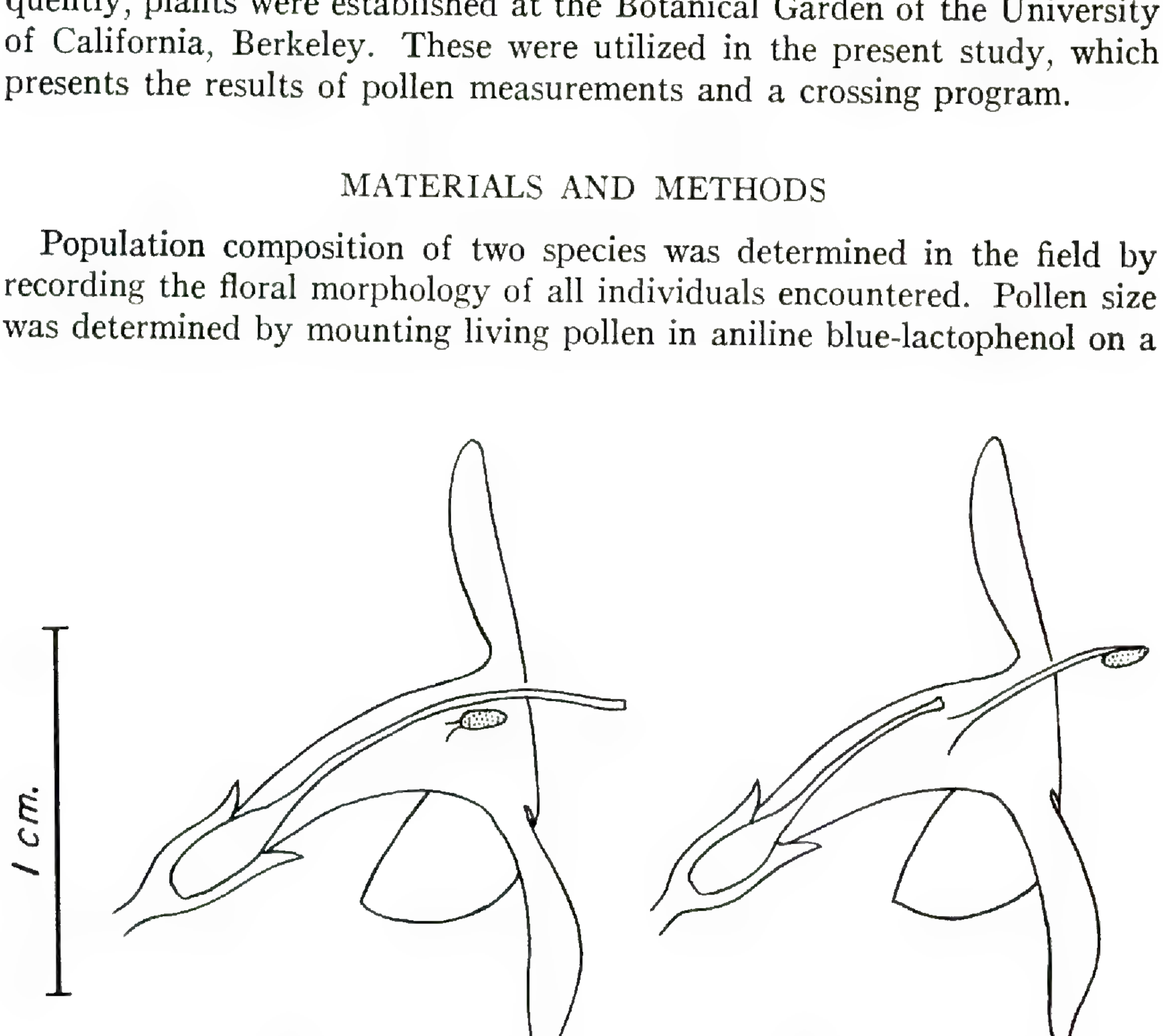

FIGURE 1. Pin and thrum flowers of **Oplonia armata** var. **pallidior** showing relative positions of anthers and stigmas of the two morphs.

glass slide and making measurements by means of an ocular micrometer. For the crossing program, flowering individuals were placed in an insect-free greenhouse, the pollinated flowers were tagged, and seed set was recorded. The following populations were utilized: *Oplonia acicularis* (Swartz) Stearn (*Ornduff 7816*, along Priestman's River, Portland Parish), *O. armata* (Swartz) Stearn var. *pallidior* Stearn (*Ornduff 7813*, cultivated plants on the University of West Indies campus, Kingston, originally from Lucea, Hanover Parish, and *Ornduff 7815*, between Bengal Bridge and Discovery Bay, Hanover Parish), and *O. microphylla* (Lam.) Stearn (*Ornduff 7814*, Four Mile Wood, St. Thomas Parish).

RESULTS

POPULATION COMPOSITION. A survey of a population of *Oplonia microphylla* (*7814*) produced 20 plants with long-styled ("pin") flowers and 16 plants with short-styled ("thrum") flowers ($Z = 0.667$); that of a population of *O. armata* var. *pallidior* (*7815*) yielded 18 pin plants and 13 thrum plants ($Z = 0.898$). Thus, the figures for both populations, when subjected to the Z test, indicate that the pin : thrum ratio was 1 : 1.

POLLEN CHARACTERISTICS. Pin pollen grains of *Oplonia microphylla* averaged 39.8 μm. in diameter (sample size (N) = 60; range = 35.1–44.9), and thrum grains averaged 45.8 μm. (N = 60; range = 41.0–54.6); both failed to stain positively with iodine-potassium iodide (IKI). Pin pollen grains of *O. armata* var. *pallidior* averaged 59.8 μm. in diameter (N = 60; range = 50.7–72.2), and thrum grains averaged 46.2 μm. (N = 60; range = 41.0–54.6); both stained positively with IKI.

POLLINATIONS. Self- and intramorph pollinations of *Oplonia armata* var. *pallidior* produced an average of 2.6 seeds per pollination, while intermorph pollinations produced 2.5 (TABLE 1), indicating that in this variety distyly is not accompanied by self-incompatibility. Within *O. microphylla* intramorph pollinations produced an average of 1.7 seeds per pollination, and intermorph pollinations produced an average of 2.7 (TABLE 1), suggesting that in this species distyly is accompanied by a weak incompatibility system.

DISCUSSION

The occurrence of heterostyly in *Oplonia* is unique in the Acanthaceae, a large and diverse family of approximately 250 genera (Airy Shaw, 1973), and in the Bignoniales (*sensu* Thorne, 1976). Unlike most heterostylous plants of other, unrelated families, *Oplonia* has strongly zygomorphic flowers and a weak or absent incompatibility system. Also in several heterostylous taxa examined, thrum pollen stains positively with IKI while pin pollen does not (Ornduff, unpubl.). The pollen of both morphs of *O. armata* var. *pallidior* stains positively, unlike that of *O. microphylla*. The significance of these intermorph differences in pollen stainability is unknown.

TABLE 1. **Results of intra- and intermorph pollinations of Oplonia species.**

TAXON	COLLECTION	CROSS	NUMBER OF FLOWERS POLLINATED	NUMBER OF SEEDS OBTAINED	AVERAGE NUMBER OF SEEDS PER POLLINATION
O. armata var. *pallidior*	*Ornduff 7813*	Pin selfed	32	94	2.9
		Pin × pin	22	47	2.1
			54	141	2.6
		Thrum selfed	19	44	2.3
		Thrum × thrum	9	26	2.9
			28	70	2.5
		Total intramorph	82	211	2.6
		Pin × thrum	33	95	2.9
		Thrum × pin	17	30	1.8
			50	125	2.5
O. microphylla	*Ornduff 7864*	Pin selfed	1	1	1.0
		Pin × pin	5	9	1.8
			6	10	1.7
		Thrum selfed	6	10	1.7
		Thrum × thrum	—	—	—
		Total intramorph	18	30	1.7
		Pin × thrum	9	27	3.0
		Thrum × pin	6	14	2.3
			15	41	2.7

During the several hours spent in the field examining populations of *Oplonia*, only one flower visitor was noted — a pierid butterfly of the species *Phoebis sennae* (L.). It is probable that the large-flowered species are pollinated by lepidopterans, since the arched, exserted stamens of thrums and the similarly exserted styles of pins suggest that intermorph pollination is mediated by insects that alight on the corolla but whose bodies are positioned some distance in front of it.

The nature of the floral morphology of *Oplonia acicularis* is puzzling. The description by Stearn (1971) suggests that the flowers are not distylous. The flowers are small (ca. 5 mm. long); examination of those collected from several plants indicates that some plants produce flowers with stigmas positioned opposite or below the anthers, and others produce flowers with stigmas positioned slightly above the anthers. Under insect-free conditions and without artificial pollination, one of the two plants of the former type and one of four plants of the latter produced fruits. It is likely that *O. acicularis* possesses a slight degree of distyly, that self-incompatibility is absent in this species, and that stigmas and anthers are sufficiently close in some individuals that spontaneous self-pollination takes place.

Despite the fact that *Oplonia armata* var. *pallidior* seemingly lacks an incompatibility system, the 1 : 1 pin : thrum ratio in the single natural population examined suggests that it is effectively outcrossed.

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PINUS MAXIMINOI: ITS TAXONOMIC STATUS AND DISTRIBUTION [1]

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BENTHAM DESCRIBED the species *Pinus tenuifolia* in 1842 from Hartweg's specimen number *620* (type), collected in Guatemala. Apparently, however, he was unaware that the name *P. tenuifolia* had already been published by Salisbury in 1796. Shaw (1909), also unaware of the earlier homonym, reduced *P. tenuifolia* to varietal status. Martínez (1948) restored *P. pseudostrobus* var. *tenuifolia* to specific status as *P. tenuifolia* Bentham. Loock (1950) followed Martínez's classification of *P. tenuifolia*; however, Standley and Steyermark (1957) did not agree with Martínez or Loock, rejected both Shaw's and Bentham's assignments, and reduced Bentham's *P. tenuifolia* and Shaw's *P. pseudostrobus* var. *tenuifolia* to synonymy under *P. pseudostrobus* Lindley. Gaussen (1960), in agreement with Martínez and Loock, restored *P. tenuifolia* to specific status. Schwerdtfeger (1953), Aguilar (1961), and Mirov (1961) followed Martínez and Loock in treating *P. tenuifolia* Bentham as a species. Molina (1964) listed only four pines (*Pinus ayacahuite* Ehrenberg, *P. oocarpa* Schiede, *P. caribaea* Morelet, and *P. pseudostrobus*) native to Honduras and made no mention of *P. tenuifolia*. More recently, Mittak (1977) treated *P. tenuifolia* as a species and also referred to intrusions of the hypoderm into the chlorenchyma in leaves collected in Guatemala.

Moore (1966) proposed *Pinus Maximinoi* H. E. Moore, nom. nov., to replace Bentham's name because of the existence of the 1796 homonym, *P. tenuifolia* Salisbury. Moore's statement is quoted here for additional information and clarity:

"PINUS

Pinus Maximinoi H. E. Moore, nom. nov.

Pinus tenuifolia Bentham, Plantae Hartwegianae 92, 1842, not *P. tenuifolia* Salisbury, 1796.

Martinez recognized *Pinus tenuifolia* Bentham as a distinct species in both editions of Los Pinos Mexicanos (1945, 1948) and the species has recently been offered for cultivation in the United States. Because *Pinus tenuifolia* is a later homonym, a new name must be provided. It is a personal pleasure to associate with this species the name of the late Prof. Maximino Martinez, who during his lifetime devoted so much attention to *Pinus* and who was ever ready to help botanists visiting Mexico."

While Moore's proposal to provide the name *Pinus maximinoi* H. E. Moore in place of the later homonym *P. tenuifolia* Bentham resolves the

[1] The research for this paper was partially covered by Rockefeller Foundation Grant no. RF78024, allocation no. 2, made through North Carolina State University to J. P. Perry, Jr.

matter of a new name for this taxon, it does not answer the questions raised by Standley and Steyermark (1958) regarding their inability "to separate it [*P. tenuifolia* Bentham] from *P. pseudostrobus*, either specifically or varietally, as it was treated by Shaw. Martínez uses the character of the association of the cone with an oblique peduncle as the principal means of separating *P. tenuifolia* from *P. pseudostrobus*. We have not found this or other characters stressed by Martínez to hold true for use in distinguishing *P. tenuifolia* from *P. pseudostrobus*."

We believe that the information that follows will clarify the differences between *Pinus maximinoi* and *P. pseudostrobus* and will establish the status of *P. maximinoi* as a distinct species.

Shaw (1909), in his description of *Pinus pseudostrobus* var. *tenuifolia*, noted "peduncles persistent on the cones; hypoderm of the leaves remarkably developed, extending from the epiderm to the endoderm and forming partitions across the green tissue." He also noted that he found leaves without the hypoderm protrusions and the persistent cone-peduncle character unreliable. Martínez (1948) noted similar characteristics for *P. tenuifolia* and mentioned the occurrence of forms that appear to be intermediate between *P. tenuifolia*, *P. pseudostrobus*, and *P. douglasiana* Martínez. Loock (1950) reported this species occurring in Mexico in the temperate warmer to subtropical zone at elevations of 1500 to 2100 meters. He pointed out that while *P. tenuifolia* is very closely related to *P. pseudostrobus*, the internal structure of the leaves of *P. tenuifolia* is quite distinct, and referred to the deep intrusions of the hypoderm into the chlorenchyma, at times extending from the epiderm to the endoderm. He also noted that the cone scales of *P. tenuifolia* are much thinner than those of *P. pseudostrobus*, and that the oblique, weak peduncle of the cone in *P. tenuifolia* nearly always accompanies it when it falls.

Schwerdtfeger (1953) and Aguilar (1961) gave detailed descriptions of *Pinus tenuifolia* and *P. pseudostrobus* and apparently experienced no difficulty in distinguishing between the two species.

In their treatment of *Pinus tenuifolia* as a synonym of *P. pseudostrobus*, Standley and Steyermark (1958) noted that the resin ducts are medial but made no mention of the characteristic protrusions of the hypoderm into the chlorenchyma in the leaves of *P. tenuifolia*. Shaw (1909), Martínez (1948), and Loock (1950) all noted this as one of the important characteristics separating *P. tenuifolia* from *P. pseudostrobus*.

Molina (1964), in his description of *Pinus pseudostrobus* in Honduras (here treated as *P. tenuifolia*), made no mention of the internal structure of the leaves, nor did he refer to the characteristic oblique peduncle that usually accompanies the cone when it falls. He did note that the cones have peduncles or are subsessile: "estrobilos caedizos, pedunculados o subsesiles. . . ."

In their 1974 study of terpene composition of Honduran pines attacked by the bark beetle *Dendroctonus frontalis*, Coyne and Critchfield concluded that one of the three host species of pines "identified as *P. pseudostrobus* in the past, is a related taxon of unsettled status: *P. tenuifolia*

Benth. or *P. pseudostrobus* var. *tenuifolia* Shaw." Their study of this pine led them to conclude that it conforms closely to *Pinus tenuifolia*, as described by Schwerdtfeger (1953), Aguilar (1961), and Martínez (1948), in leaf structure and cone characteristics. They also noted that *P. pseudostrobus* seen in several localities in Guatemala appeared to be uniformly different from *P. tenuifolia* studied in Honduras, while *P. tenuifolia* observed in Guatemala and the state of Oaxaca, Mexico, closely resembled *P. tenuifolia* in Honduras. They pointed out that the majority of fallen cones of *P. tenuifolia* had the peduncle attached. In about half the trees examined, they found the mesophyll of some needles partitioned by one to three hypodermal intrusions that extended to the endodermis; they noted that "the partitions were not associated with the resin canals, and most were extensions of the abaxial hypodermis."

A comparison of the oleoresin components of *Pinus maximinoi* and *P. pseudostrobus* also reveals significant differences between the two species. Coyne and Critchfield (1974, *table 1*) showed terpene composition of oleoresin from three Honduran pines, *P. oocarpa*, *P. caribaea*, and *P. tenuifolia*. Recently, Vité (pers. comm.) and Brümmer (1978) have reported on analyses of oleoresin from *P. maximinoi* and *P. pseudostrobus* collected in Guatemala in the departments of Sololá and Guatemala. The analyses were made by Brümmer as a part of her master's degree thesis at the University of Hamburg. This information is presented in TABLE 1, along with Coyne and Critchfield's data on analysis of oleoresin collected from *P. maximinoi* in Honduras.

The analyses of oleoresin from Coyne and Critchfield's Honduran *Pinus maximinoi* and that from Brümmer's Guatemalan *P. maximinoi* are remarkably similar. They differ markedly from that of *P. pseudostrobus* in the amount of α- and β-pinenes present. Mirov's (1961) analysis of *P. tenuifolia* (considered here to be *P. maximinoi*) oleoresin is quite different from the analyses shown here. His sample, collected in the state of Michoacán, Mexico, was composed of 77 percent α-pinene, 6–7 percent β-pinene, 8 percent Δ^3 carene, 1–2 percent terpinolene, 3 percent dipentene, ca. 1 percent linaloöl, less than 1 percent methyl chavicol, and 1 percent sesquiterpenes. Unfortunately, his analysis of *P. pseudostrobus* oleoresin was not completed.

We have collected examples of *Pinus maximinoi* and have examined it in the field in all of the Mexican states where it has been reported to occur (Sinaloa, Jalisco, Michoacán, Guerrero, Oaxaca, Chiapas); we have also observed it in the states of Morelos, Puebla, Hidalgo, and Veracruz. During the years 1950–1958, Perry had an opportunity to examine Martínez's specimens of *P. tenuifolia* and *P. pseudostrobus* at the Instituto de Biología in Mexico. Mittak has collected and examined *P. maximinoi* and *P. pseudostrobus* at a number of locations in Guatemala. Both authors have collected and observed *P. maximinoi* in Honduras; Perry has also collected it in northern and central El Salvador at elevations ranging from 1500 to 1800 meters. More recently (May, 1978), we collected numerous examples of *P. maximinoi* at 1400 to 1780 meters elevation in the depart-

TABLE 1. **Mean terpene composition of xylem oleoresin from Pinus maximinoi and P. pseudostrobus.**

Type of compound	Terpene	Coyne and Critchfield (1974)* *P. maximinoi*	Brümmer (1978)† *P. maximinoi*	Brümmer (1978)† *P. pseudostrobus*
ALKANE	Tricyclene	—	t	0.4% (+)
ALDEHYDE	α-pinene	54.2	52.8% (+++)	93.7% (+++)
	Camphene	0.6	0.7% (+)	0.8% (+)
	β-pinene	39.2	35.3% (+++)	0.6% (+)
	Sabinene	—	0	0.6% (+)
ESTER	Myrcene	2.7	2.8% (+)	0.5% (+)
AROMATIC	Δ^3-carene	≤0.5	0.7% (+)	0.5% (+)
MONOTERPENE	Limonene	1.4	0.8% (+)	0.5% (+)
HYDROCARBONS	β-phellandrene	1.5	1.4% (+)	t
	γ-terpinene	0	0	0
	Terpinolene	0	t	0.2% (+)
	Allo-ocimene	0	t	t
	α-terpinene	0	t	0
OXYGENATED MONO- AND SESQUITERPENES	Campholelenaldehyde	—	0	t
	Linaloöl	—	t	1.9% (+)
	Bornylacetate	—	0	t
	Methyl chavicol	—	1.7% (+)	1.3% (+)
	Longifolene	—	t	0
	M-204‡	—	t	0
	β-caryophyllene	—	0.3% (+)	0
SESQUITERPENE	Humelene	—	t	0
HYDROCARBONS	γ-muurolene	—	t	0
	M-204	—	2.5% (+)	0
	α-muurolene	—	t	0
	δ-cadinene	—	t	0
	γ-cadinene	—	t	0

* In their publication, no information was presented on oxygenated mono- and sesquiterpenes, sesquiterpene hydrocarbons, tricyclene, or sabinene.

† The following symbols are taken from Brümmer (1978): (+++) principal component, (++) subcomponent, (+) low concentrations, (t) trace.

‡ M-204 is a new, unidentified compound found by Brümmer (1978).

ment of Baja Verapaz, Guatemala, on the federal forest property located a few kilometers from the town of San Jerónimo (FIGURE 1). This is the same area in which Hartweg collected the type specimen of *Pinus tenuifolia*. The trees were growing in association with *P. oocarpa* Schiede, *P. tecumumani* Schwerdt. (this species was clearly described by Schwerdtfeger in 1953, but without a Latin description), *Liquidambar styraciflua L.*, and *Quercus* spp.

From our extensive field observations, comparisons of *Pinus maximinoi* and *P. pseudostrobus*, and examinations of a great many leaf sections in the laboratory, we find Martínez's (1948) and Loock's (1950) descriptions of *P. tenuifolia* (referred to here as *P. maximinoi*) complete and very reliable when used for field identification of the species. We have, of course, examined specimens with cones and foliage that varied from the typical form of the species, but that is usual for many of the variable Mexican species of pines (Zobel & Cech, 1957; Mirov, 1967).

When Critchfield (Coyne & Critchfield, 1974) visited pine stands in Michoacán, Mexico, the problem of separating *Pinus pseudostrobus* and *P. maximinoi* was apparently complicated by the presence of *P. douglasiana* and *P. martinezii* Larsen. Perry has collected extensively in Michoacán and has observed all the species referred to above both in the field and (with the exception of *P. martinezii*) in Martínez's collections in Mexico City. While the cones of *P. maximinoi*, *P. martinezii*, and *P. douglasiana* do resemble one another, the cones of *P. maximinoi* are usually smaller and lighter than those of the other two species, and its cone scales are thinner and more flexible with the apophyses flatter and more appressed. The leaves of *P. maximinoi* are much more slender (0.5–0.7 mm. vs. 0.7–1.0 mm.) than those of *P. douglasiana* and *P. martinezii* and are always flexible and drooping; those of both of the latter species are stiff, erect, and never drooping. In addition to these differences, the leaves of *P. martinezii* are borne in fascicles of 5, 6, and 7, mostly 6, while those of *P. maximinoi* and *P. douglasiana* are borne mostly in fascicles of 5. In *P. maximinoi* the branchlets are quite smooth, with the bases of the leaf bracts widely spaced and soon merging into the bark. In both *P. martinezii* and *P. douglasiana* the branchlets are rough and scaly due to the decurrent bases of the leaf bracts, which are scaly and prominent. Martínez's photograph and drawings (1948, pp. 180, 181) illustrate this characteristic very clearly. Finally, in *P. maximinoi* and *P. douglasiana* the peduncle generally falls with the cone, and the hypoderm forms protrusions that extend to the endoderm (FIGURE 2); in *P. martinezii* and *P. pseudostrobus* the peduncle, together with a few basal cone scales, remains attached to the branch when the cone falls, and the hypoderm never forms protrusions. A summary of the outstanding differences between *Pinus maximinoi* and *P. pseudostrobus* is shown in TABLE 2.

With regard to the range of *Pinus maximinoi*, Shaw (1909) stated that *P. pseudostrobus* var. *tenuifolia* occurs in Mexico (in the states of Sinaloa, Durango, Jalisco, Michoacán, Oaxaca, and Chiapas), Guatemala, and northwestern Nicaragua. Martínez (1948) and Loock (1950) cited its occurrence in the Mexican states of Guerrero, Sinaloa, Michoacán, Jalisco, Oaxaca, and Chiapas. Standley and Steyermark (1958) stated that *P. pseudostrobus* L. (*P. tenuifolia* and *P. pseudostrobus* var. *tenuifolia* listed

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FIGURE 1. Well-stocked stand of *Pinus maximinoi* on the federal forest property at 1450 meters elevation, located a few kilometers from the town of San Jerónimo, Baja Verapaz, Guatemala.

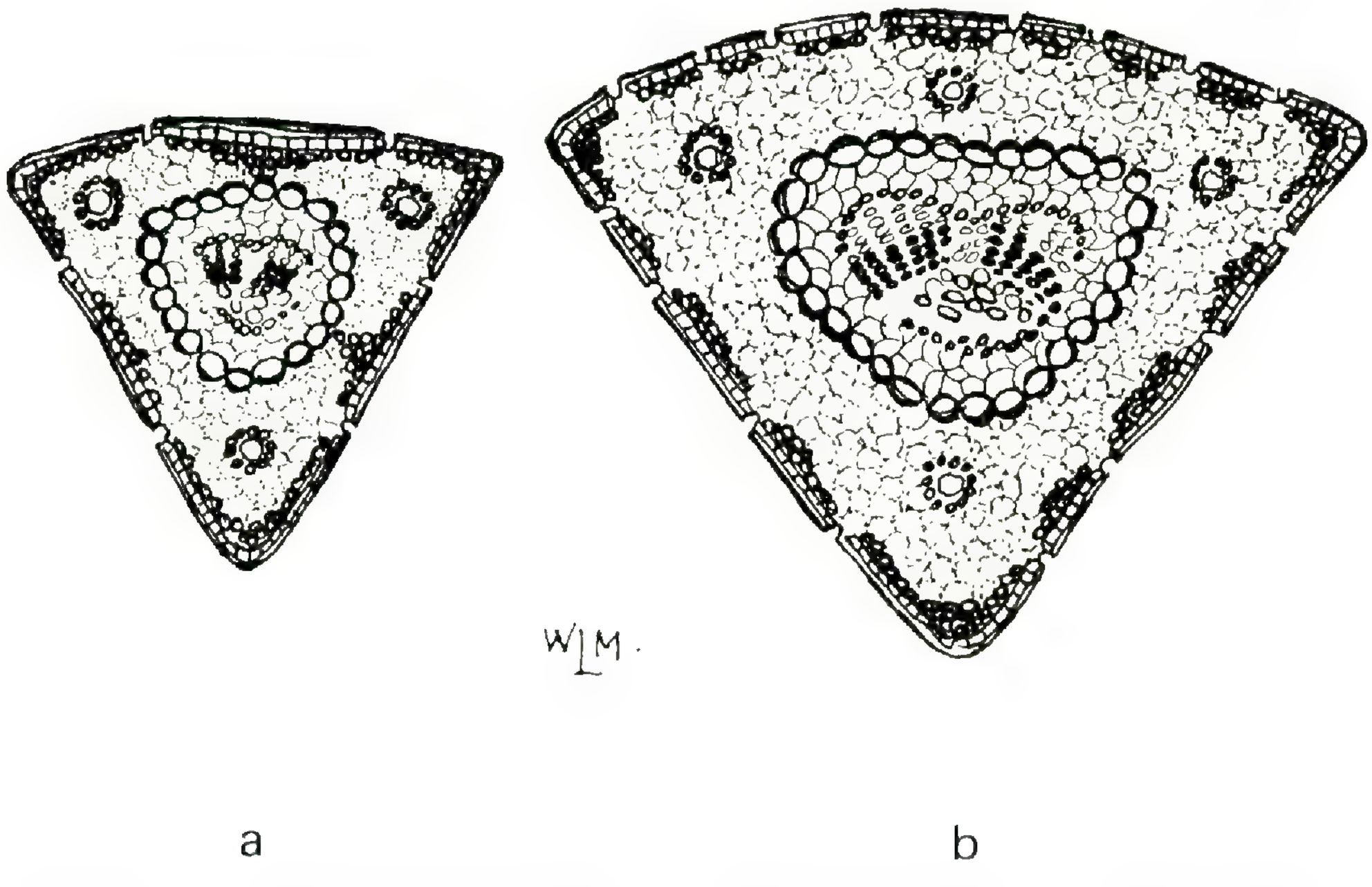
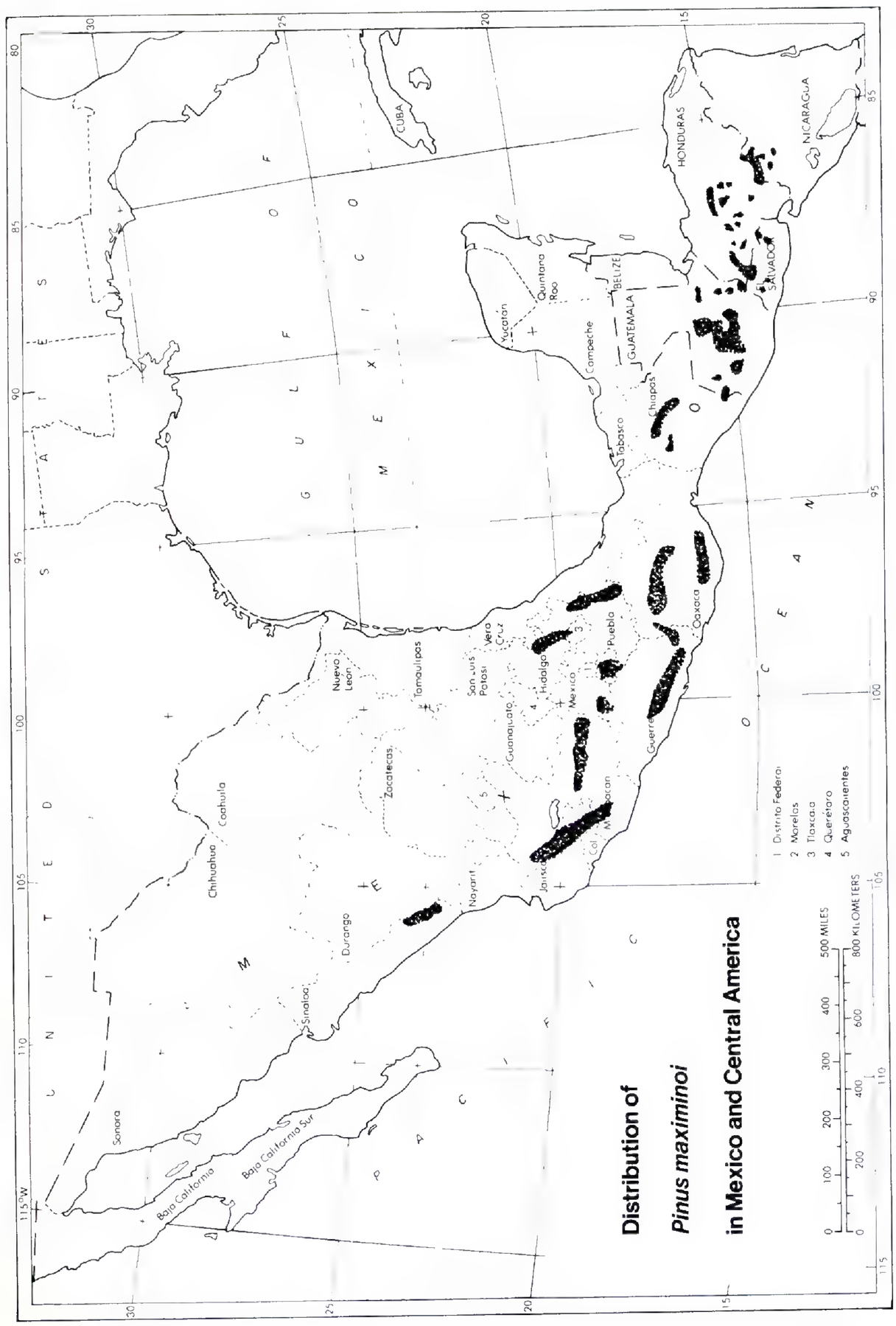


FIGURE 2. Cross section of needles: a, *Pinus maximinoi*; b, *P. pseudostrobus*; both × 60.

as synonyms) occurs in a number of departments in Guatemala and in Belize, Honduras, and Nicaragua. Mirov (1961) reported its occurrence in central and southern Mexico (Jalisco, Michoacán, Sinaloa, Guerrero, Puebla, Veracruz, Chiapas) and Guatemala. Taylor (1963, *fig. 4*, p. 33) showed *P. pseudostrobus* (treated here as *P. maximinoi*) extending into the central highland region of Nicaragua along the border of Honduras.

Critchfield and Little (1966) showed the distribution of "*P. pseudostrobus*, including the doubtfully distinct *P. tenuifolia* Benth. (not Salisb.)" from Sinaloa and Nuevo Léon through central and southern Mexico as far south as northwestern Nicaragua. Their *map 52* shows one collection point barely inside the northern boundary of El Salvador, and the collector is cited as "unpublished P. H. Allen 1962 (El Salvador)." In the herbarium of the Escuela Panamericana at Zamorano, Honduras, the authors examined *P. H. Allen 7324* (*P. pseudostrobus*), collected May 6–7, 1959, at Los Esemiles, area east of La Palma, department of Chalatenango, El Salvador, at 6000–7500 feet. Unfortunately no cones were present with the specimen, but the very slender needles more closely resembled those of typical *P. maximinoi* than those of *P. pseudostrobus*. Perry has collected extensively in the department of Chalatenango, El Salvador, and has not found a single specimen of *P. pseudostrobus*; he has, however, observed a number of small stands of *P. maximinoi* mixed with *P. oocarpa*.

In their recent publication, Coyne and Critchfield (1974) noted that *Pinus pseudostrobus* might be expected to extend from Guatemala into Honduras on the higher mountains, but in the mountains northeast and southwest of Tegucigalpa, Honduras, at elevations of 1250 and 2000 meters, they observed only *P. tenuifolia*.


Distribution of
Pinus maximinoi
in Mexico and Central America
CUBA
HONDURAS
NICARAGUA
SALVADOR
GUATEMALA
BELIZE
Quintana Roo
Yucatan
Campeche
Tabasco
Chiapas
Oaxaca
Guerrero
Puebla
Mexico
Hidalgo
Vera Cruz
San Luis Potosi
Guanajuato
Tamaulipas
Nuevo Leon
Zacatecas
Coahuila
Chihuahua
Durango
Nayarit
Jalisco
Sinaloa
Sonora
Baja California
Baja California Sur
1 Distrito Federal
2 Morelos
3 Tlaxcala
4 Queretaro
5 Aguascalientes
0 100 200 300 400 500 MILES
0 200 400 600 800 KILOMETERS

MAP 1.

TABLE 2. **Summary of differences between Pinus pseudostrobus and P. maximinoi.**

CHARACTER	*P. pseudostrobus*	*P. maximinoi*
Cones	Larger, heavier	Smaller, lighter
Cone scales	Thick, stiff; apophyses generally slightly raised	Thin, flexible; apophyses generally flat to depressed
Peduncle	Usually remaining attached to branch with a few basal cone scales	Oblique; generally falling with the cone
Leaves		
Dimensions	17–32 cm. long, to 1 mm. thick	15–28 cm. long, to 0.7 mm. thick
Internal structure	Resin canals 3 or 4, medial; no hypodermal intrusions	Resin canals 2 or 3, medial; hypodermal intrusions generally extending to endoderm
Oleoresins	α-pinene 93.7% β-pinene 0.6% Sesquiterpene components absent	α-pinene 52.8% β-pinene 35.3% Sesquiterpene components present
Altitudinal range	1600–3200 meters	700–2400 meters

From our numerous field trips in Guatemala, Honduras, and El Salvador, we believe that the southerly limit of the range of *Pinus pseudostrobus* occurs in Guatemala in the departments of Totonicapán, Quezaltenango, Sololá, Chimaltenango, Sacatepéquez, and Guatemala; we have not found a single specimen of this species south or east of these departments.

The authors' collections and field observations extend the range of *Pinus maximinoi* in Mexico to include the states of Hidalgo and Morelos; in El Salvador, the department of Chalatenango, east and west of the town of La Palma, along the Honduras boundary and the department of San Salvador on the slopes of the Volcán de San Salvador just west of the capital city, San Salvador. Also in El Salvador, Schmutzenhofer (1975) showed *P. tenuifolia* occurring in the departments of Morazán, near the towns of Perquin and San Simón, and Santa Ana, west of Lago de Coatepeque and Sonsonate, as well as on the Volcán de Santa Ana, Volcán de Izalco, and Volcán San Marcelino.

In the herbarium of the Escuela Panamericana at Zamorano, Honduras, we examined a number of pine specimens collected in Nicaragua and labeled *Pinus pseudostrobus*. The needles, however, were uniformly very slender and, from superficial examination, appeared to be those of *P. maximinoi*.

Although we have not yet had an opportunity to collect *P. maximinoi* in Nicaragua, we believe that it occurs in the northwest, as indicated by Shaw (1909) and Critchfield and Little (1966). Accordingly, we show the range of *P. maximinoi* extending into northwestern Nicaragua (Map 1).

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A NEW COMBINATION IN SYZYGIUM FOR EUGENIA MAIRE (MYRTACEAE) OF NEW ZEALAND

W. R. SYKES AND P. J. GARNOCK-JONES

THE LINNAEAN GENUS *Eugenia* has traditionally embraced a very large and varied assemblage of tropical and subtropical shrubs and trees fairly evenly divided in numbers between the Old and New Worlds. However, "most recent authors tend to segregate *Syzygium* from *Eugenia* s.l. and occasionally to accept a number of other Old World segregates: most notably *Acmena, Piliocalyx, Acicalyptus, Aphanomyrtus, Cleistocalyx, Cupheanthus* . . . , *Jambosa, Jossinia* and *Pareugenia*" (Schmid, 1972a). The majority of these segregate genera are founded on solitary or inconsistent characters and are not widely accepted. Schmid (1972a) assembled the available evidence and thoroughly discussed the characters used to separate *Syzygium* Gaertner sensu lato from *Eugenia* sensu stricto, including several anatomical ones resulting from his own studies. Schmid (1972b) accepted *Acmena* DC. and *Syzygium* as exclusively Old World segregates of *Eugenia* and relegated *Acicalyptus* A. Gray, *Cleistocalyx* Blume, *Caryophyllus* L., and *Jambosa* DC. to synonymy under *Syzygium*. *Eugenia* as thus circumscribed is concentrated in tropical America but with series Jossinia (DC.) Niedenzu in the Old World tropics.

The affinities of the endemic New Zealand species *Eugenia maire* have been considered by several workers who studied wood or bark anatomy or pollen morphology. Ingle and Dadswell (1953) discussed wood anatomy characters that separate *Eugenia* "A" from *Syzygium* sensu lato and *Eugenia* "B," and placed *E. maire* in the latter group. *Eugenia* "B" referred to species of *Eugenia* that would be better placed in *Syzygium*. Chattaway (1959) obtained similar results from a study of bark anatomy. Pike (1956) described pollen of 33 species of *Eugenia* sensu lato, mostly from the Old World. The three species of *Eugenia* "A" that she studied, none of which came from America, had longicolpate pollen, whereas her examples of *Acmena*, *Cleistocalyx*, *Eugenia* "B," *Jossinia* DC., *Piliocalyx* Brongniart & Gris, and *Syzygium* had either syncolpate or parasyncolpate pollen. McIntyre (1963) reported that pollen of *E. maire* is similar to that of *Cleistocalyx*, *Eugenia* "B," and *Syzygium*. At our request Dr. N. T. Moar has examined pollen of *Acmena smithii*, *Cleistocalyx longiflorus*, four species of *Eugenia* sensu stricto from America (including the type species), *E. maire*, *E. rariflora* (series Jossinia), and eight species of *Syzygium* (including the type species). Among these species there were no clear distinctions between genera. The pollen of *E. maire* shares features with *Cleistocalyx longiflorus* and some species of *Syzygium* and *Eugenia*, but not with *Acmena smithii* and *E. rariflora* (N. T. Moar, pers. comm.). Pollen of 32 species of *Eugenia* from central Brazil studied by Barth and Barbosa (1972) ranged from brevicolpate through parasyncolpate to syncolpate, a range of variation suggesting that Pike (1956) and McIntyre

(1963) were premature in accepting the nature of the colpi as a generic character in the Eugeniinae.

We have examined *Eugenia maire* with respect to most of the characters listed by Schmid (1972a), including all of the morphological and anatomical characters he considered significant in distinguishing between *Syzygium* sensu lato and *Eugenia* sensu stricto. Our findings, together with a summarized form of Schmid's most significant diagnostic characters, are presented in TABLE 1. We found no pentamerous perianths among the flowers of a very small sample of *E. maire*; therefore, this inconclusive result is not included in the table. However, the specimens examined by Gray (1854) had the calyx margin obscurely five-toothed; he placed *E. maire* in *Eugenia* § *Syzygium*.

Schmid (1972a) considered the pathway of the vascular supply to the ovules to be the most important of his list of diagnostic characters, *Eugenia* sensu stricto having a transeptal supply and that of *Syzygium* sensu lato being axile. Serial transverse sections of *E. maire* buds (stained with safranin and fast green) showed the following floral vascular structure (terminology follows Schmid, 1972b), diagrammatically represented in FIGURE 1. The floral tube bundles are in a monocyclic arrangement. Sclerenchyma is present as fibers, especially on the outer side of the floral tube bundles. The ovular supply is axile, formed from the coalescence of inwardly directed traces originating from the floral tube bundles low in the pseudopedicel. The axile ovular strand divides parallel to the septum

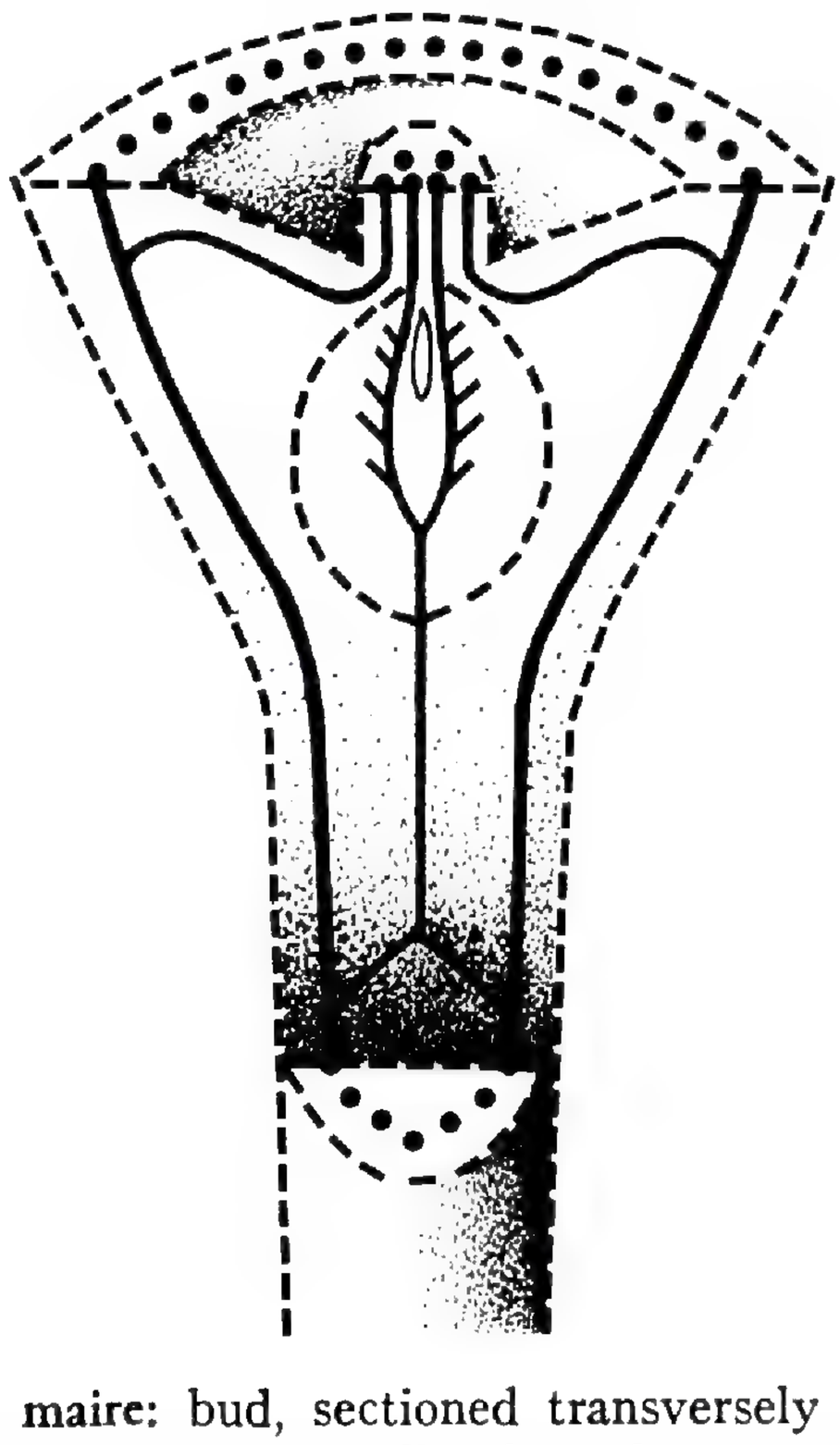

FIGURE 1. **Eugenia maire:** bud, sectioned transversely through base of style and base of pseudopedicel, longitudinally through septum (diagrammatic).

TABLE 1. Characters used to separate Syzygium from Eugenia* and their states in E. maire.

	Eugenia sensu stricto	*Syzygium* sensu lato	*E. maire*
Pubescence on vegetative and/or reproductive parts	Present on most species	Present on very few species	Absent
Position of inflorescence	Predominantly lateral	Usually terminal	Terminal
Structure of inflorescence	Solitary flowers or usually racemes	Solitary flowers, panicles, cymes	Cymes
Bracteoles subtending flowers	Mostly persistent and conspicuous	Mostly fugacious and inconspicuous	Fugacious, inconspicuous
Pseudopedicel (attenuate flower base)	Rarely present	Mostly present	Present
Corolline or calycine calyptrae	Absent	Often present; mostly corolline	Present; corolline
Cotyledons	Usually fused	Usually distinct	Distinct
Large bundles of floral tube	Monocyclic	Mono- to mostly zonocyclic	Monocyclic
Number of bundles if pattern monocyclic	Definite, usually 8	Indefinite	Indefinite
Pathway of vascular supply to ovules	Transeptal	Axile	Axile
Texture of ovarian tissue	Compact	Usually spongy	Spongy

* From Schmid, 1972a.

in the lower part of the ovary. Repeated branches from these two ovular strands supply the ovules without forming a discrete placental ring. The two major branches of the axile ovular supply skirt the compitum by following the remnants of the septum, and continue upward into the lower part of the style. They are joined at the base of the style by about six carpellary traces originating from the vascular cylinder above the ovary.

The characters in TABLE 1, especially the axile ovular supply, show that the closest affinities of *Eugenia maire* are with those Indo-Malaysian and West Pacific species that have already been transferred to *Syzygium* sensu stricto. *Eugenia maire* approaches *Acmena* in its monocyclic arrangement of floral tube bundles and lack of a placental ring, but these features are also found in a number of species of *Syzygium* (Schmid, 1972b); *E. maire* cannot be placed in *Acmena* because its anther sacs are parallel and dehisce by lateral slits. Other segregates of *Syzygium* sensu lato and the main characters they are based upon (none of which are shared with *E. maire*) are *Acicalyptus* (calyx calyptrate), *Aphanomyrtus* Miquel (stamens eight or fewer), *Cupheanthus* Seemann (calyx tube 2.5–6 cm. long), *Cleistocalyx* (calyx calyptrate), *Jambosa* (petals free), *Pareugenia* Turrill (stamen filaments fused in groups), and *Piliocalyx* (calyx calyptrate). The calyptrate corolla and incurved stamens of *E. maire* are illustrated in FIGURE 2.

Many of the necessary combinations in *Syzygium* have been made, notably by E. D. Merrill and L. M. Perry and later by Perry alone, in a series of papers quoted by Schmid (1972a). Most of these were regional monographs; there is no monograph of the genus. The solitary New Zealand species has remained in *Eugenia* since it was described.

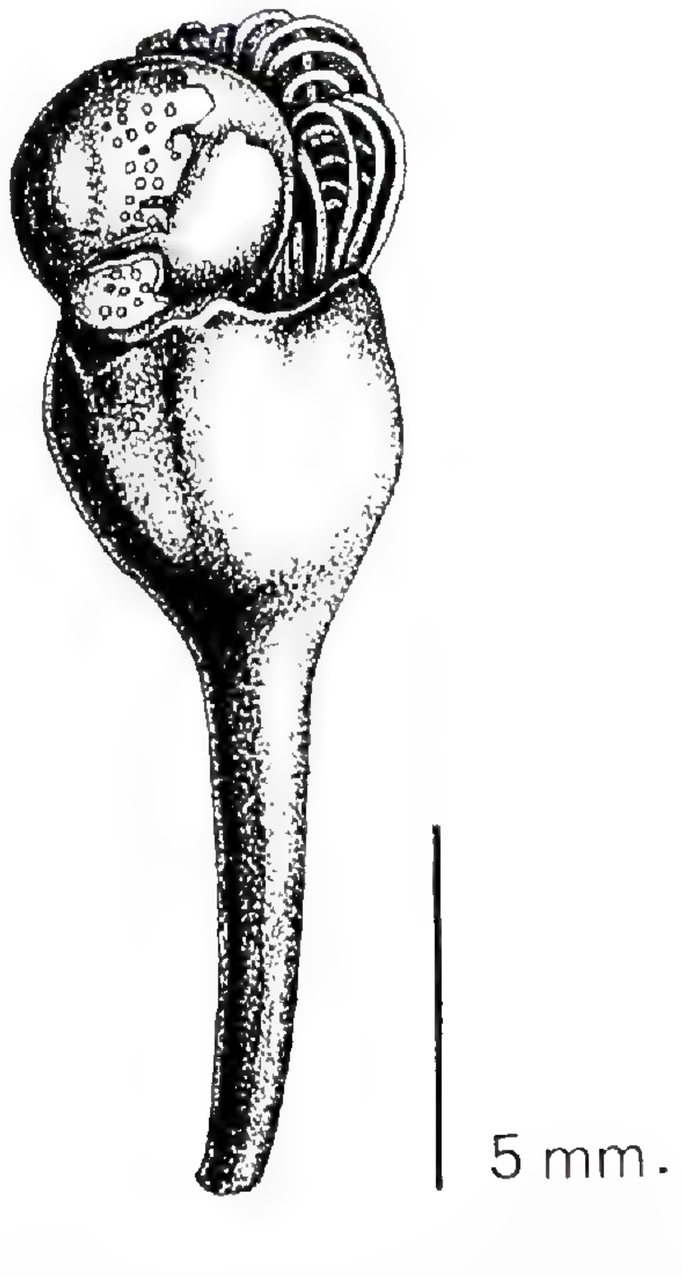

FIGURE 2. **Eugenia maire:** bud at anthesis.

Syzygium maire (A. Cunn.) Sykes & Garnock-Jones, comb. nov.

Eugenia maire A. Cunn. Ann. Nat. Hist. 3: 114. 1839. LECTOTYPE: "New Zealand, *R. Cunningham*, 1834" (K; photograph seen).

Although in the protologue A. Cunningham cited "New Zealand (Northern Island). Alluvial banks of rivers, Bay of Islands, & c. — 1833, R. Cunningham," there are no specimens so labeled at Kew, and none dated 1833 (G. E. Wickens, pers. comm.). The specimen chosen by Allan (1961) as lectotype bears the number *564*, which corresponds with the number of the species in Cunningham's protologue; consequently we have followed Allan's choice.

Two other New Zealand species originally placed in *Eugenia*, *E. obcordata* Raoul and *E. vitis-idaea* Raoul, were transferred to the endemic genera *Lophomyrtus* and *Neomyrtus*, respectively, by Burret (1941). Both genera are segregates of *Myrtus*. Their fruits contain a number of small seeds (rarely as few as two) with curved embryos, as opposed to the one or two large seeds with straight embryos in *Eugenia* and *Syzygium* fruits.

The recognition of the New Zealand maire tawake or black maire as a species of *Syzygium* extends the known range of that genus southward into the temperate South Pacific to about 41°S. In Australia the genus does not extend south of the subtropical rain forests of New South Wales, 35°S. *Syzygium* is indigenous in the Pacific as far east as Rose Island in American Samoa and, according to some authorities, Hawaii. Species of *Eugenia* series Jossinia are also indigenous to the tropical South Pacific, and one, *E. rariflora* Bentham, the type of which is from Fiji (sometimes included in *E. reinwardtiana* (Blume) DC.) extends across much of tropical Polynesia. Such species are shrubs, sometimes semiprostrate, or small spreading trees with axillary flowers, solitary or few together forming a small fascicle, with prominent petals and fused cotyledons. They are very distinct from any Polynesian or Fijian species of *Syzygium*.

Syzygium maire and some other species (including *Dysoxylum spectabile* (Forster f.) Hooker f., two species of *Elaeocarpus* L., *Litsea calicaris* (A. Cunn.) T. Kirk, *Planchonella novo-zelandica* (F. Mueller) Allan, and *Schefflera digitata* J. R. & G. Forster) are outliers in New Zealand of large widespread genera in the Indo-Malaysian and tropical West Pacific regions. They are mostly lowland North Island trees and provide evidence of an affinity between the floras of New Zealand and the tropical regions to the north and northwest.

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Dr. I. A. E. Atkinson, Botany Division, D.S.I.R., Lower Hutt, Dr. R. O. Gardner, Botany Division, D.S.I.R., Auckland, and Mrs. K. Reynolds, Whangarei, provided fresh buds of *Syzygium maire* which were sectioned and stained by E. J. Beuzenberg and illustrated by Robyn Conway, both of Botany Division, D.S.I.R., Christchurch. Dr. G. E. Wickens, of the

Royal Botanic Gardens, Kew, provided photographs of R. Cunningham's herbarium specimens of *Syzygium maire*, and Dr. N. T. Moar of Botany Division, D.S.I.R., Christchurch, reported on an examination of the pollen of 16 species of *Eugenia* and related genera.

To all these people we express our thanks.

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BOTANY DIVISION
DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH
CHRISTCHURCH, NEW ZEALAND

Preliminary Announcement

Thirteenth International Botanical Congress

Sydney, Australia. 21-28th August, 1981

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COVER: The buds, leaves, and fruit of *Carpinus caroliniana* Walter, hornbeam or blue beech, form the basis of this year's cover design. An individual nutlet, together with its leafy, three-lobed wing, will appear on the offprints; a series of these was used in designing the device that appears on the back cover. The designs were all drawn by Karen Stoutsenberger from materials collected from plants growing in the Arnold Arboretum.

Widespread in the Northern Hemisphere, *Carpinus* L. (placed in the Betulaceae or alternatively in the Corylaceae or even the Carpinaceae), with upwards of 35 species, exhibits a disrupted Arcto-Tertiary distribution in eastern North America, Europe, Asia Minor, and in eastern Asia where the center of species diversity occurs. The only North American representative of the genus, *C. caroliniana* grows along the edges of streams and in wet, rich soils in forested areas from Nova Scotia and Quebec southward to Florida and westward into Minnesota, Iowa, Missouri, eastern Texas, and Oklahoma. Disjunct populations are known in mountainous regions of southern Mexico and in Central America.

The stems of *Carpinus caroliniana*, a small tree, have smooth, brownish- or bluish-gray, sinuate bark and an appearance reminiscent of those of beech trees (*Fagus* spp.). The wood, which is occasionally used for tool handles, is light brown to nearly white. Its growth habit, relatively small size, conspicuous infructescences, and foliage, which turns deep scarlet and orange to yellow in fall, combine to make this species an attractive native ornamental. — *S. A. S.*

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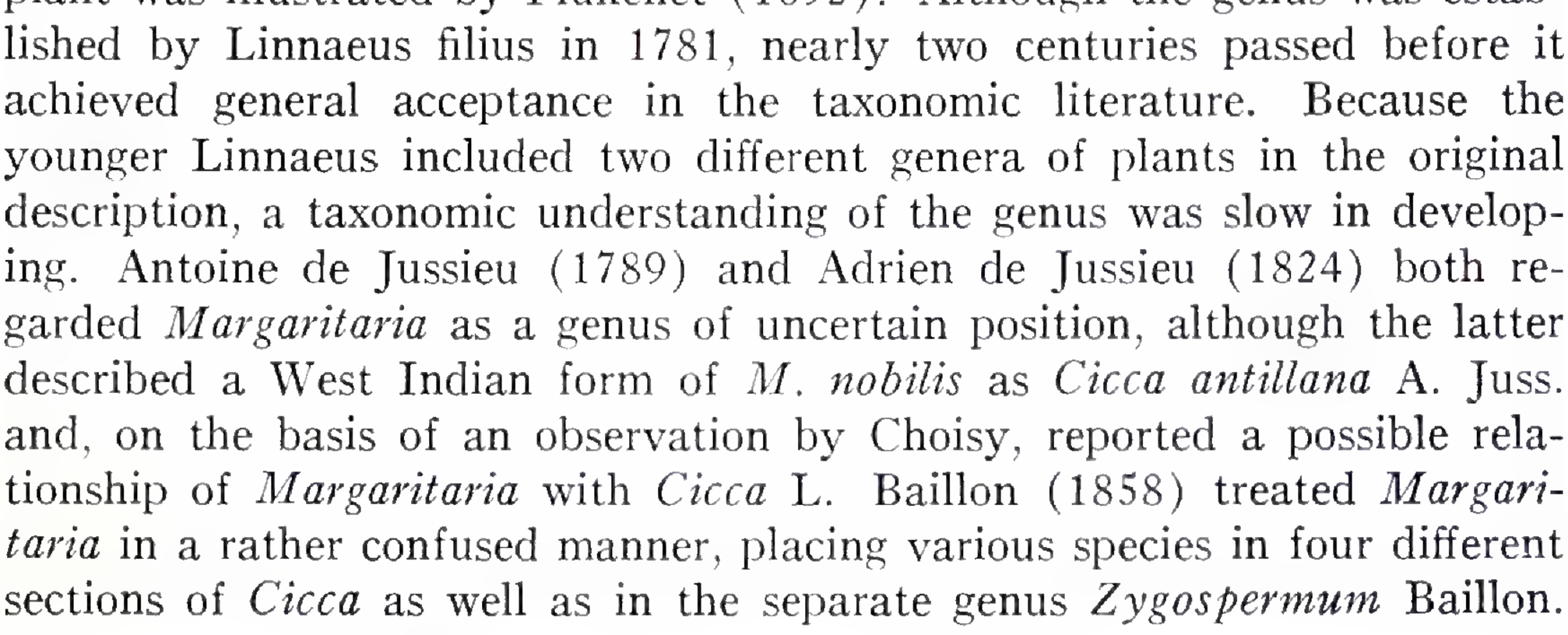
A REVISION OF MARGARITARIA (EUPHORBIACEAE)

GRADY L. WEBSTER

AMONG THE SMALLER GENERA of Euphorbiaceae subfamily Phyllanthoideae Pax, *Margaritaria* has a particularly broad distribution (MAP 1) in both the New and Old World tropics (except for the Pacific islands). The name (in the form *Margaritifera*), alluding to the characteristic pearly white endocarp of the fruit, was first used by Hermann (1689), and the plant was illustrated by Plukenet (1692). Although the genus was established by Linnaeus filius in 1781, nearly two centuries passed before it achieved general acceptance in the taxonomic literature. Because the younger Linnaeus included two different genera of plants in the original description, a taxonomic understanding of the genus was slow in developing. Antoine de Jussieu (1789) and Adrien de Jussieu (1824) both regarded *Margaritaria* as a genus of uncertain position, although the latter described a West Indian form of *M. nobilis* as *Cicca antillana* A. Juss. and, on the basis of an observation by Choisy, reported a possible relationship of *Margaritaria* with *Cicca* L. Baillon (1858) treated *Margaritaria* in a rather confused manner, placing various species in four different sections of *Cicca* as well as in the separate genus *Zygospermum* Baillon.



MAP 1. World distribution of *Margaritaria* (generalized). Base maps from Goode series, © University of Chicago.

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Mueller Argoviensis (1866) continued this association between *Cicca* and *Margaritaria* but clarified the relationships to some extent by removing *Cicca disticha* (= *Phyllanthus acidus* (L.) Skeels) to a separate subsection of *Phyllanthus* sect. *Cicca* (L.) Mueller-Arg.

Baillon and Mueller saw that the Old World taxa described under *Prosorus* Dalz. by Dalzell (1852) and Thwaites (1856) were related to the New World *Margaritaria*. However, they failed to realize that the taxa *Margaritaria/Prosorus* do not belong in close juxtaposition with *Cicca* (*sensu stricto*). Bentham (1880), who rejected *Margaritaria* as being founded on a mixture of taxa, did point out that *Prosorus* was discordant with *Cicca* because of its tricarpellate fruit. Hooker (1887) judiciously maintained *Cicca* and *Prosorus* as separate sections of Indian *Phyllanthus*. However, this felicitous disposition of Hooker was ignored by Pax (1890) and Pax and Hoffmann (1931), who lumped *Cicca* and *Margaritaria* together in *Phyllanthus* sect. *Cicca*. Although occasional writers of floras (e.g., Britton & Millspaugh, 1920; Gamble, 1924) maintained *Margaritaria* or *Prosorus* as distinct genera, most conservative botanists have followed the usage of Mueller and of Pax, at least until the rehabilitation of *Margaritaria* by Webster (1957) and Airy Shaw (1966).

As I have pointed out earlier (Webster, 1957, 1968), *Margaritaria* is really quite distinct from *Phyllanthus* (including *Cicca*) and indeed is closer to *Flueggea* Willd. in Phyllantheae subtribe Flueggeinae Mueller-Arg. (Webster, 1975). The unique seeds, with fleshy exotesta and thick, bony endotesta, separate *Margaritaria* from all other Phyllantheae. The fruits of most species of *Margaritaria*, with a brittle, irregularly shattering, papery endocarp (FIGURES 5, 6), are equally distinctive. Staminate material of *Margaritaria* may be distinguished from that of *Flueggea* by the lack of a pistillode, and from that of *Phyllanthus* by the annular disc subtending a tetramerous androecium. The resemblance with *Phyllanthus* sect. *Cicca* that impressed 19th century botanists is very superficial indeed, since *Cicca* differs markedly in its drupaceous fruits with thin-walled, dry seeds and in its very different vegetative structure (with typical phyllanthoid branching, the ultimate axes being short lived and deciduous, in contrast to the persistent, unspecialized branches of *Margaritaria*).

Morphologically, the species of *Margaritaria* are all rather similar, and the dioecious character of the plants makes it rather difficult to construct workable keys to individual specimens. Most taxa are deciduous shrubs or small trees that grow in seasonal forest or bush vegetation. The habit of *Margaritaria* agrees with that of many other unspecialized Euphorbiaceae; Hallé *et al.* (1978) cite *M. discoidea* as an example of the architectural model of Roux, in which the sapling axis has spiral phyllotaxy but the leaves on the branchlets are distichous. To judge from my own observations of *M. nobilis* as well as from indications in the literature, all of the species in the genus would seem to belong to the model of Roux. The entire leaves, with short petioles and distinct stipules, vary relatively slightly in morphology. Flowers, often produced at the proximal nodes

of expanding new axes, are usually in anthesis before the current crop of leaves is mature. Opler, Frankie, and Baker (1976) have reported that in the seasonal forest in Guanacaste, Costa Rica, *M. nobilis* flowers about two weeks after the first spring rain in April or May, and only remains in flower about three days. Other *Margaritaria* populations in African and Asian monsoon forests may show similar flowering behavior. The tetramerous calyx is rather similar in all species, and the annular floral disc is so constant that it provides a good generic character. In all normal staminate flowers (FIGURE 12), the stamens are consistently 4, and the filaments are nearly always free. The tricolporate, semitectate pollen grains of *Margaritaria* are typical of many unspecialized Phyllantheae and are very similar to those of such genera as *Flueggea* (Punt, 1962; Köhler, 1965).

The pistillate flowers of *Margaritaria* (FIGURES 11, 13) have calyx and disc similar to that of the staminate. The main differential characters are found in the ovary, which has from 2 to 6 carpels. Mueller (1866) used carpel number as a diagnostic character in defining subsections of his sect. *Cicca*, but its value in indicating phylogenetic relationships is not very great. Carpel number has been independently reduced to 2 in the West Indies (*M. hotteana*), the Indian Ocean islands (*M. anomala*), and Australia (*M. dubium-traceyi*); within the American *M. nobilis* it fluctuates from 3 to 6 in such an unstable manner that it cannot be used to define subspecific taxa. However, despite some overlap, the pattern of carpel number distribution is distinctively different in *M. nobilis* and the closely related *M. discoidea* (TABLES 1, 2).

The fruits of most species of *Margaritaria* are different from those of all other Phyllantheae. The endocarp is thin, papery, and hyaline, and easily shatters to expose the fleshy seeds (FIGURES 5, 6). The seeds are even more distinctive, with their metallic blue-green, fleshy sarcotesta (exotesta), bony sclerotesta (endotesta), and large hilum. These seeds would appear to be morphologically adapted for bird dispersal; van der Pijl (1969), in fact, discusses *M. nobilis* as an example of "deceitful" ornithochorous seeds (although the sarcotesta is sufficiently thick that the notion of deceit is perhaps here misplaced). The sclerotesta of the seed furnishes a useful systematic character, since it varies considerably in size and sculpturing. It is distinctively rugose in *M. indica* and *M. rhomboidalis*, but smooth in most other taxa.

Cytologically, *Margaritaria* appears to be diploid with a base number of 13 ($2n = 26$), like many unspecialized taxa of subfamily Phyllanthoideae (Webster & Ellis, 1962; Mangenot in Bancilhon, 1971). Although there are only two published counts (for *M. discoidea* and *M. nobilis*), the uniformity of the genus makes it appear unlikely that additional counts would reveal any significant cytological diversity.

Ecologically, species of *Margaritaria* might fairly be characterized as plants of secondary successions in tropical, seasonal climates, although they may also be found in climax or evergreen forests. Adjanohoun (1964) reported that *M. discoidea* is common in secondary stages of moist forest

TABLES 1, 2. **Carpel number variation in American and African taxa of Margaritaria.**

1. Carpel numbers of individual fruits (all specimens pooled).

Species	Number of collections	Number of fruits	Percentage of fruits with carpel number 2	3	4	5	6
M. nobilis							
West Indies	34	290	0	2.8	28.6	67.2	1.4
Mesoamerica	53	462	0	12.6	78.4	8	1.1
South America	113	1025	0	4.2	68.5	25.3	2.0
Overall	200	1777	0	6.1	64.6	27.6	1.7
M. discoidea							
subsp. *discoidea*	71	1405	1.4	88.3	10.3	0	0
subsp. *nitida*	34	294	1.4	97.0	1.4	0	0
Overall	105	1699	1.4	89.8	8.7	0	0
M. obovata	16	240	21.7	77.5	0.8	0	0

2. Distribution of carpel number by collections.

	3	3/4	4	4/5	5	5/6	6	3/4/5	4/5/6	3/4/5/6	Total
M. nobilis											
West Indies	1	1	2	18	8	1	0	1	2	0	34
Mesoamerica	1	16	24	7	2	3	0	0	0	0	53
South America	0	15	31	39	12	6	0	4	5	1	113
Overall (%)	1	16	28.5	32	11	5	0	2.5	3.5	0.5	200

	2	2/3	3	3/4	4	2/3/4	Total
M. discoidea							
subsp. *discoidea*	0	2	44	24	0	1	71
subsp. *nitida*	0	2	29	2	0	1	34
Overall (%)	0	3.8	69.5	24.8	0	1.9	105
M. obovata (%)	0	50	43.8	6.2	0	0	16

in West Africa but also invades savannas. To judge from the data on herbarium specimens, *M. nobilis* displays a similar ecological amplitude in America.

Analysis of specimens from the great areas inhabited by *M. nobilis*, *M. discoidea*, and *M. indica*, in America, Africa, and Asia, respectively, shows a considerable amount of ill-defined fluctuating morphological variability, as one might expect to find in extensive panmictic populations. Only in Africa is there more than one distinct mainland continental species. Speciation has occurred mainly in the Caribbean and Indian Ocean islands and thus appears to reflect a "peripheral" effect; i.e., the definitive geo-

graphic segregation of islands seems to have been prerequisite to speciation, at least outside Africa.

Reconstruction of phylogenetic relationships in *Margaritaria* must be based mainly on comparison of living species, in view of the paucity and questionableness of the fossil evidence. Mädel (1962) has noted the resemblance between the wood of the Upper Cretaceous *Paraphyllanthoxylon* and the living *Margaritaria discoidea*. Bailey (1924) established the genus *Paraphyllanthoxylon* on the basis of similar Cretaceous wood from Arizona; more recently Cahoon (1972) has described *P. alabamense* from Cenomanian/Turonian rocks in central Alabama. The large diameter (1 m. or more) of some of the Alabama logs is so uncharacteristic of living species of *Margaritaria* that the generic assignment appears dubious; in fact, even if these various Cretaceous "species" of *Paraphyllanthoxylon* are euphorbiaceous, it is doubtful if one could defend a closer systematic assignment than simply the tribe Phyllantheae. Since the pollen of *Margaritaria* is no more distinctive than the wood, it seems unlikely that forthcoming paleobotanical evidence will offer any clues very useful in reconstructing the phylogeny of the genus.

The morphological diversity found in Africa and Madagascar indicates that this region may be designated as the most likely homeland for *Margaritaria*, as was suggested earlier for another genus of Phyllantheae, *Meineckia* Baillon (Webster, 1965). The ornithochorous dispersal of *Margaritaria* would seem to allow a fairly high probability for successful transoceanic long-distance migration; however, the failure of the genus to invade the Pacific islands suggests that its dispersibility may be somewhat limited. As far as the intercontinental distribution of *Margaritaria* is concerned, there does not appear to be enough evidence for a decision to be made between the alternative models of transoceanic dispersal or migration over rafting tectonic plates. However, when the distribution patterns of other Phyllantheae such as *Meineckia* and *Flueggea* are taken into account, one may perhaps best explain the distribution of *Margaritaria* by postulating both expansions and contractions from a once more nearly continuous range (probably achieved without extensive long-distance dispersal).

SYSTEMATIC TREATMENT

Margaritaria Linnaeus f. Suppl. Pl. 66. 1781. *Cicca* sect. *Pseudo-Cicca* Baillon, Étude Gén. Euphorb. 618. 1858. *Phyllanthus* sect. *Cicca* subsect. *Paracicca* Mueller-Arg. Linnaea 32: 50. 1863. *Phyllanthus* sect. *Cicca* subsect. *Margaritaria* (L. f.) Mueller-Arg. in DC. Prodr. **15**(2): 414. 1866. TYPE: *Margaritaria nobilis* L. f.

Prosorus Dalz. Jour. Bot. Kew. Misc. **4**: 345. 1852. *Cicca* sect. *Prosorus* (Dalz.) Baillon, Étude Gén. Euphorb. 619. 1858. *Phyllanthus* sect. *Cicca* subsect. *Prosorus* (Dalz.) Mueller-Arg. in DC. Prodr. **15**(2): 416. 1866. *Phyllanthus* sect. *Prosorus* (Dalz.) Hooker f. Fl. Brit. India **5**: 305. 1887. TYPE: *Prosorus indicus* Dalz. (= *Margaritaria indica* (Dalz.) Airy Shaw).

FIGURES 1–4. Leaf bases of *Margaritaria*: 1, *M. scandens* (*Correll 43522*), showing adaxially channeled petiole, × 5; 2, *M. hispidula* (*Appert 107*), showing nonchanneled petiole, × 8; 3, *M. rhomboidalis* (*Leandri et al. 2195*), showing adaxially channeled petiole, × 8; 4, *M. luzoniensis* (*Otanes 17955*), showing nonchanneled petiole, × 8.

Zygospermum Thwaites ex Baillon, Étude Gén. Euphorb. 620. 1858. TYPE: *Zygospermum zeylanicum* Thwaites ex Baillon (= *Margaritaria cyanosperma* (Gaertner) Airy Shaw).

Wurtzia Baillon, Adansonia I. **1:** 186. *t. 7, figs. 5, 6.* 1861. TYPE: *Wurtzia tetracocca* Baillon (= *Margaritaria tetracocca* (Baillon) Webster).

Cicca sect. *Ciccoides* Thouars ex Baillon, Étude Gén. Euphorb. 618. 1858. *Phyllanthus* sect. *Cicca* subsect. *Ciccoides* Mueller-Arg. in DC. Prodr. **15**(*2*): 418. 1866. TYPE: *Cicca anomala* Baillon (= *Margaritaria anomala* (Baillon) Fosberg).

Calococcus Kurz ex Teijsm. & Binn. Nat. Tijdschr. Nederl. Ind. **27:** 48. 1864. TYPE: *Calococcus sundaicus* Kurz ex Teijsm. & Binn. (= *Margaritaria indica* (Dalz.) Airy Shaw).

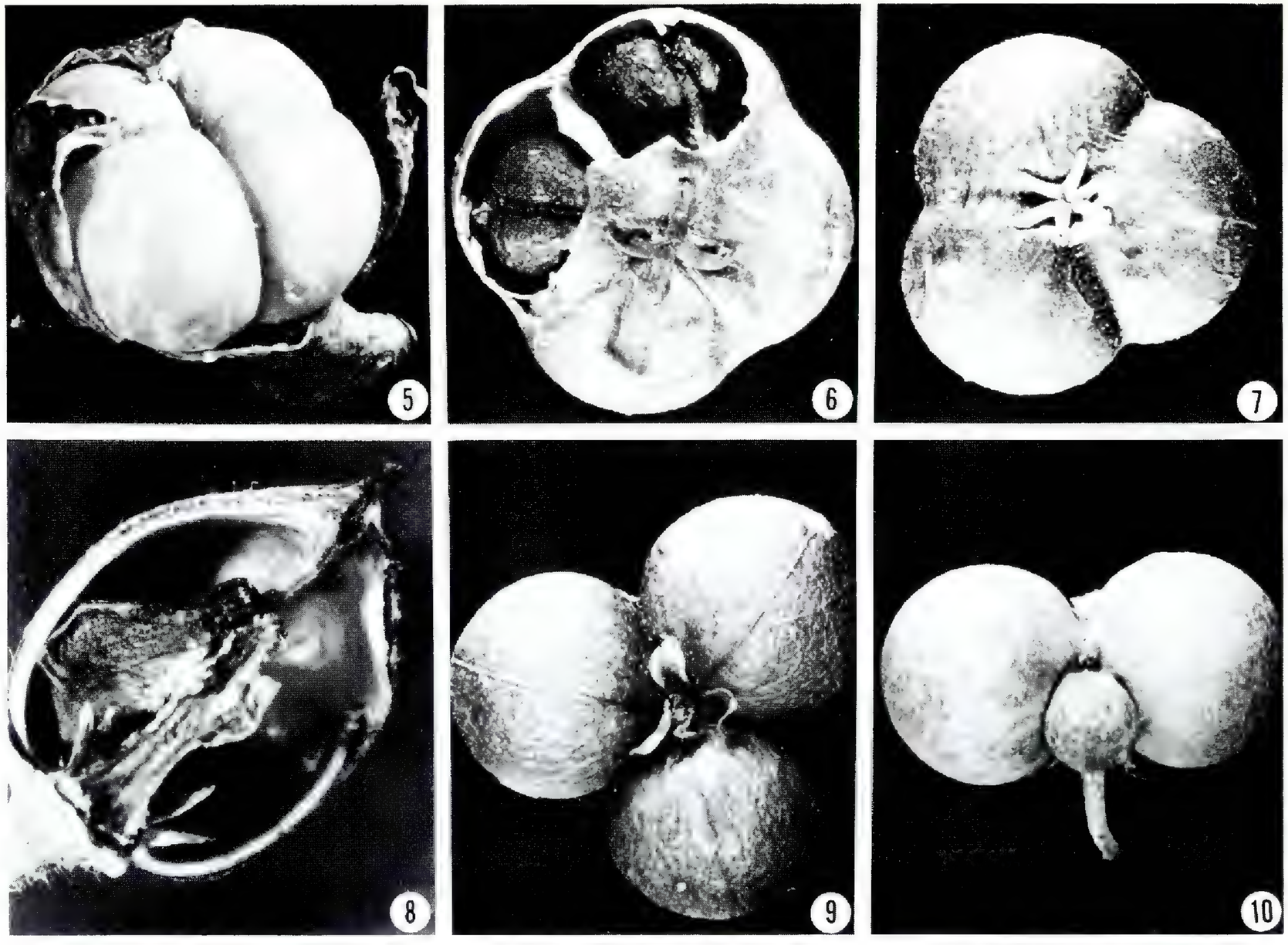
Dioecious shrubs or trees (rarely scandent); foliage usually deciduous, new leaves appearing with flowers (or sometimes evergreen); phyllotaxy on branches distichous; branches persistent, bark usually lenticellate in age. Leaves mostly chartaceous, pinnately veined; veins brochidodromous; margins entire; petioles short; stipules entire or denticulate, deciduous or subpersistent. Flowers in clusters at proximal axils of expanding leafy branches (or on short shoots); pistillate (occasionally) and staminate (rarely) flowers solitary. Staminate flower: pedicel elongated, often capillary, not articulated; sepals 4, biseriate, often unequal (outer pair usually narrower), membranous or chartaceous, entire or denticulate, midvein usually sparsely branched; disc annular, entire or shallowly lobed, adnate to base of calyx (reduced or absent in a few taxa); stamens 4, the filaments free (rarely basally connate), the anthers extrorse in bud, dehiscing longitudinally, muticous; pollen grains subglobose, 3-colporate, semitectate; pistillode absent. Pistillate flower: pedicel terete or flattened, not articulated; calyx and disc similar to staminate; ovary with 2 to 6 carpels, the styles free or basally connate, bifid to bipartite, often somewhat dilated, ovules 2 per locule, hemitropous. Fruit capsular, more or less irregularly dehiscent, the green exocarp separating from the thin, papery endocarp (in most taxa); seeds normally paired in each locule, the outer coat (sarcotesta) fleshy, bluish, the inner coat (sclerotesta) thick, woody or bony, smooth or rugose, invaginated at the chalazal end, the endosperm copious, whitish, the embryo straight or slightly curved, with cotyledons thin and flat, much longer than the radicle.

As here interpreted, *Margaritaria* is a relatively homogeneous genus of 14 species that are all rather closely related. The most distinctive group is Baillon's section *Ciccoides*, with 2-carpellate fruits that do not have a thin, papery endocarp (FIGURE 8). Although *M. dubium-traceyi* of Australia has similar fruits, it does not appear to be immediately related to *M. anomala* of Madagascar and the Mascarenes, the type of sect. *Ciccoides*. It does not seem expedient, therefore, to recognize any subgeneric taxa within *Margaritaria*.

KEY TO THE SPECIES OF MARGARITARIA

1. Ovary glabrous, or if hirtellous then not deeply lobed.
   2. Filaments free.
      3. Fruits irregularly dehiscent, the endocarp thin, hyaline, papery.

4. Endotesta of seed smooth or nearly so.
5. Branch tips not spinose.
6. Branches glabrous or hirsutulous but not finely scabridulous; stipules lanceolate, not basally cordate.
7. Petioles adaxially channeled; leaf blades rounded to acuminate; young twigs glabrous or hirsutulous.
8. Carpels mostly 4 or 5 (rarely 3 or 6); styles free or nearly so; stipules 2–5 mm. long; seeds 2–4 mm. long; leaves usually acuminate. ..... 1. *M. nobilis.*
8. Carpels mostly 3 (rarely 2 or 4); stipules 5–10 mm. long or if shorter then styles distinctly connate; leaves rounded to acuminate. ... 2. *M. discoidea.*
7. Petioles not adaxially channeled; leaf blades obtuse or rounded at tip; young twigs reddish hirsutulous; carpels 3. ..... 6. *M. luzoniensis.*
6. Branches usually finely scabridulous; stipules lanceolate or ovate, basally cordate, cuspidate-acuminate; carpels 3 or 4.
9. Anthers 0.5–0.7 mm. long; staminate disc over 1 mm. across; carpels mostly 3; leaves more or less glaucous beneath, stipules pale. ..... 3. *M. scandens.*
9. Anthers 1.2–1.4 mm. long; staminate disc obsolete; carpels mostly 4; leaves not glaucous beneath, stipules dark and indurate. ..... 4. *M. tetracocca.*
5. Branch tips slender, spinescent, scabridulous when young; stipules lanceolate, pale; carpels 2. ..... 5. *M. hotteana.*
4. Endotesta of seed distinctly rugose or ribbed; carpels 3; plants glabrous.
10. Staminate disc well developed; veinlet reticulum not distinctly prominulous; carpels 3.
11. Staminate calyx lobes 1–1.6 mm. long; anthers 0.5–1 mm. long; pistillate flowers often 2 or 3 per axil. ..... 7. *M. indica.*
11. Staminate calyx lobes 3.3–3.7 mm. long; anthers 1.8–2 mm. long; pistillate flowers solitary. ..... 8. *M. cyanosperma.*
10. Staminate disc obsolete or absent; veinlet reticulum distinctly prominulous; carpels 2 or 3. ..... 9. *M. rhomboidalis.*
3. Fruits tardily dehiscent, the endococci not extremely thin and hyaline; leaves mostly rounded to emarginate; carpels 2.
12. Leaves and fruits glabrous.
13. Endotesta of seed smooth; leaf venation not prominulous; anthers 0.8–1.4 mm. long. ..... 10. *M. anomala.*
13. Endotesta of seed rugose; leaf venation prominulous; anthers 0.3–0.5 mm. long. ..... 11. *M. dubium-traceyi.*
12. Leaves and fruits hispidulous or hirsutulous; leaf venation prominulous. ..... 12. *M. hispidula.*
2. Filaments distinctly connate; leaves not over 2 cm. long, rounded to emarginate; carpels 2 or 3, glabrous. ..... 13. *M. decaryana.*
1. Ovary hirtellous (rarely glabrous), deeply lobed, 1 or 2 of the 3 carpels often abortive; petioles not adaxially channeled; endococci hyaline-papery. ..... 14. *M. obovata.*



FIGURES 5–10. Fruits of *Margaritaria*. 5, 6, *M. nobilis* (*Gentle 508*): 5, 4-carpellate fruit, exocarp peeling back to expose papery endocarps; 6, endocarps of 2 carpels broken away to show paired seeds inside; both × 5. 7, *M. discoidea* subsp. *discoidea* (*Linder 125*), intact 3-carpellate fruit, × 5. 8, *M. hispidula* (*Appert 107*), longitudinal section of fruit showing firmly adherent endocarp, × 7. 9, 10, *M. obovata* (*Mwasumbi LMB 10477*): 9, 3-carpellate fruit; 10, fruit with third carpel abortive; both × 4.5.

1. **Margaritaria nobilis** Linnaeus f. Suppl. Pl. 428. 1781. *Phyllanthus nobilis* (L. f.) Mueller-Arg. in DC. Prodr. **15**(2): 414. 1866. TYPE: Surinam, *Dahlberg s.n.* (LINN). FIGURES 5, 6.

Margaritifera arbor Sirinamensis Hermann, Paradisi Batavi Prodr. 352. 1689. *Euonymus Margaritifera pentacoccus Americana* Plukenet, Phytographia, *t. 176, fig. 4.* 1692.

Margaritaria alternifolia L. in Alm, Pl. Surinam. 16. 1755, *nomen illegit.*

Cicca antillana A. Juss. Euphorb. Gen. Tent. 108. *t. 4, fig. 13B.* 1824. *Phyllanthus antillanus* (A. Juss.) Mueller-Arg. Linnaea **32:** 51. 1863. *Phyllanthus antillanus β pedicellaris* Mueller-Arg. *ibid. Phyllanthus nobilis antillanus* (A. Juss.) Mueller-Arg. in DC. Prodr. **15**(2): 415. 1866. *Margaritaria nobilis* var. *antillana* (A. Juss.) Stehlé & Quentin, Catal. Fl. Guad. **2:** 47. 1937. TYPE: St. Thomas, *Riedlé s.n.* (P-JU).

Cicca surinamensis Miq. Linnaea **21:** 479. 1848. *Phyllanthus antillanus α concolor* Mueller-Arg. Linnaea **32:** 51. 1863. TYPE: Surinam, *Hostmann 622* (U, lectotype).

Cicca pavoniana Baillon, Étude Gén. Euphorb. 618. 1858. *Phyllanthus nobilis ζ pavonianus* (Baillon) Mueller-Arg. in DC. Prodr. **15**(2): 415. 1866. TYPE: Peru, *Pavon s.n.* (P, holotype, *n.v.*; G, isotype).

Cicca antillana var. *γ pedicellaris* Griseb. Mem. Am. Acad. II. **8:** 158. 1860. TYPE: Cuba, Farallones, *Wright 584a* (GOET, holotype; G, GH, S, isotypes).

Phyllanthus nobilis β guyanensis Mueller-Arg. in DC. Prodr. **15**(2): 414. 1866. TYPE: French Guyana, *Sagot 1153* (G, holotype; U, isotype).

Phyllanthus nobilis γ peruvianus Mueller-Arg. in *ibid.* TYPE: Peru, *Spruce 4472* (G, holotype).

Phyllanthus nobilis δ brasiliensis Mueller-Arg. in *ibid.* TYPE: Brazil, Minas Gerais, *Claussen s.n.* (G, holotype; A, isotype).

Phyllanthus nobilis ε riedelianus Mueller-Arg. in *ibid.* TYPE: Brazil, *Riedel s.n.* (*n.v.*).

Phyllanthus nobilis var. *θ martii* Mueller-Arg. Fl. Brasil. **11**(2): 70. 1873. TYPE: Brazil, *Martius 2813* (M).

Phyllanthus nobilis var. *panamensis* Mueller-Arg. *ibid.* TYPE: Panama, *Sutton Hayes 749* (M, lectotype).

Phyllanthus heteromorpha Rusby, Descr. S. Am. Pl. 42. 1920. TYPE: Colombia, *H. H. Smith 1716* (NY, holotype; MO, U, isotypes).

Phyllanthus nobilis var. *hypomalacus* Standley, Carnegie Inst. Publ. **461:** 68. 1935. *P. antillanus* var. *hypomalacus* (Standley) Lundell, Phytologia **1:** 337. 1939. TYPE: Mexico, Campeche, *Lundell 897* (F).

Celastrus tetramerus Standley, Contr. U. S. Natl. Herb. **23:** 679. 1923. TYPE: Mexico, Iguala Canyon, *Pringle 10319* (US).

Deciduous shrub or tree to 20 meters high; branches glabrous or rarely hirtellous, subterete or angled, becoming prominently lenticellate; foliage deciduous (perhaps sometimes evergreen). Leaf blades chartaceous, elliptic or oblong to oblanceolate, mostly 6–15 cm. long, 2.5–5 cm. broad, acuminate, obtuse to cuneate at base, decurrent on petiole, glabrous or sometimes hirsutulous beneath along the veins, sometimes glaucous beneath; major veins mostly 7 to 12 on a side, veinlet reticulum prominent beneath but scarcely prominulous; margins plane; petiole ca. 2–5 mm. long, distinctly channeled adaxially; stipules caducous to more or less

persistent, pale and scarious, elliptic- to oblong-lanceolate, acuminate, 1.5–3(–4.5) mm. long. Staminate flowers several per axillary cluster; pedicels ca. 2.5–8 mm. long, glabrous; sepals biseriate, glabrous, 0.9–1.7 mm. long, 0.7–1.5 mm. broad (outer pair usually narrower); disc 1–2 mm. across; stamens 4, free, filaments becoming 1–2 mm. long, the anthers elliptic or oblong, 0.5–1.1 mm. long. Pistillate flowers 1 to several per axil; pedicels subterete, glabrous, becoming 5–12(–16) mm. long; sepals 4, biseriate, the inner ones 1.5–2.5 mm. long, 1.5–2.5 mm. broad (outer ones usually narrower); disc 0.8–2.5 mm. across; ovary usually of 4 (65%) or 5 (28%) (rarely 3 or 6) carpels, not deeply lobed, the styles free or basally connate, 1.5–3 mm. long, bifid. Fruits subglobose to oblate, moderately lobed, 7.5–11 mm. in diameter, dehiscing irregularly, endocarps papery; seeds with thick, bluish green sarcotesta, the endotesta smooth, planoconvex, (2–)2.7–4 mm. long, 1.9–3.7 mm. broad.

DISTRIBUTION. Seasonal, rain, or riparian forests, mostly at lower elevations (up to 1000 meters); Mexico and Cuba south to Peru and Brazil (MAPS 2, 3).

REPRESENTATIVE SPECIMENS (cited to indicate range limits). **Mexico.** JALISCO: 2.5–4 mi. N. of La Cuesta, *McVaugh et al. 21190* (DAV, MICH). SAN LUIS POTOSÍ: Tamazunchale, *Lundell & Lundell 7259* (A). **Central America: Belize.** Corozal, *Gentle 508* (MO, US). **Guatemala.** *Petén, Lundell 3432* (GH). **El Salvador.** Chalaltenango, *Allen 7040* (F, US). **Honduras.** YORO: Morazán, *Webster et al. 12000* (DAV). SWAN IS.: Great Swan, *Proctor 32543* (DAV). **Nicaragua.** Volcán Santiago, *Maxon 7680* (GH, US). **Costa Rica.** Limón, *Shank & Molina 4199* (F, US). **Panama.** Barro Colorado Is., *Foster 1192* (DAV, MO). **West Indies: Cuba. LAS**

MAP 2. Distribution of *Margaritaria* in the Caribbean. Solid dots, *M. nobilis*; squares, *M. tetracocca*; solid stars, *M. scandens*; open stars, *M. hotteana*.

VILLAS: Buenos Aires, *Jack 7401* (A). ORIENTE: Río Yao, *Webster 4150* (DAV, GH); Farallones, *Wright 584a* (GH); Charco de Toro, *Wright 1933* (GOET). PINAR DEL RÍO: Mendoza, *Ekman 18086* (NY). **Haiti.** Morne Birgonne, *Ekman H2627* (A). **Dominican Republic.** Monción, *Ekman H12997* (DAV, S). **Puerto Rico.** Fajardo to Luquillo, *Sintenis 1553* (GH). **Jamaica.** Troy, *Harris 8698* (GH). **Virgin Islands.** ST. THOMAS, *Eggers 173* (GH). ST. JOHN, *Raunkiaer s.n.* (C). **Lesser Antilles.** ANTIGUA: Blubber Valley, *Box 1493* (A). GUADELOUPE: Vieux-Fort, *Webster, Ellis, & Miller 9157* (DAV, MICH, U). DOMINICA: Carholm Estate, *Ernst 1949* (DAV, US). MARTINIQUE: Ste.-Luce, *Hahn 964* (GH). SABA: *Boldingh 2198* (U). ST. LUCIA: Morne la Sorcière, *Proctor 18169* (DAV). ST. VINCENT: Letchwood Valley, *Beard 613* (A, NY, U). GRENADA: Union, *Proctor 17174* (A, DAV, U). GRENADINES: Mustique, *G. W. Smith 128* (GH). **Tobago.** Scarborough, *Broadway 4043* (GH, S, U). **Trinidad.** Cedros, *Broadway TRIN 7411* (TRIN). **South America: Colombia.** Puerto Berrio, *Haught 2180* (A, US). **Venezuela.** Isla Margarita, *Johnston 332* (GH); Delta Amacuro, *Wurdack & Monachino 39689* (US). **Guyana.** Kanuku Mts., *A. C. Smith 3509* (A, U, US). **Surinam.** Paramaribo, *Kappler 1625* (MO). **French Guiana.** Cayenne, *Broadway 345* (GH, US). **Ecuador.** El Recreo, *Eggers 15744* (S, US). **Peru.** Iquitos, *Asplund 14631* (US). **Bolivia.** Buenavista, *Steinbach 7374* (A). **Paraguay.** Estrella, *Hassler 10906* (M). **Argentina.** Posadas, *Ekman 1460* (S). **Brazil.** SANTA CATARINA: Itajai, *Klein 959* (US).

This widespread species is rarely abundant in any one locality, since it appears to belong to successional stages of vegetation. It displays a considerable amount of morphological variation, and Mueller in his final treatment (1873) recognized no less than nine varieties, of which seven were confined to various regions of South America. After considerable study of the available specimens, I have concluded that it is not profitable to attempt to demarcate any subspecific taxa, since the variation in morphological characters appears to be clinal, without any prominent discontinuities. Pubescent forms, designated by Standley as *Phyllanthus nobilis* var. *hypomalacus*, occur promiscuously mixed with glabrous ones. There is a tendency for 3-carpellate fruits to occur more commonly in Mexico and Central America, but they also occur in Paraguay and sporadically elsewhere; 5- and even 6-carpellate fruits are found in the Amazon basin and Colombia, but many West Indian specimens are also largely 5-carpellate (TABLES 1, 2).

The nomenclature and typification of this widespread American species of *Margaritaria* presents several problems. Linnaeus (in Alm, 1775) described two species, *M. oppositifolia* and *M. alternifolia*, that are illegitimate because the generic name *Margaritaria* was not validly published at that time. In 1781 Linnaeus filius assigned a different name, *M. nobilis*, probably because he combined the two taxa of 1775 (even though he expressed doubt about their conspecificity). It is not evident which specimen of those in the Linnaean Herbarium was collected by Dahlberg (as cited in the protologue), but I believe that the sheet labeled *M. alternifolia* can reasonably be taken to be the holotype. Wheeler (1939, a, b) suggested that both the generic name and the specific epithet of *Margaritaria nobilis* should be rejected because of the original inclusion of discordant elements; but under current rules of nomenclature, it appears

MAP 3. South American distribution of *Margaritaria nobilis*.

that Mueller (1866) salvaged the names by excluding the combretaceous element and thus achieving a satisfactory typification.

2. **Margaritaria discoidea** (Baillon) Webster, Jour. Arnold Arb. **48**: 311. 1967. *Cicca discoidea* Baillon, Adansonia I. 1: 85. 1860. *Phyllanthus discoideus* (Baillon) Mueller-Arg. Linnaea 32: 51. 1863; in DC. Prodr. **15**(2): 416. 1866. TYPE: Gambia, Albreda, *Heudelot 102* (P, lectotype).

Shrubs or trees to 20 (rarely 30) meters high; branches subterete or angled, glabrous or hirsutulous when young, becoming prominently lenticellate; foliage usually deciduous. Leaf blades chartaceous, elliptic or oblong, mostly acute to acuminate at apex, acute to obtuse at base, mostly 3–15 cm. long, 2–4(–5.5) cm. broad, glabrous beneath or sometimes hir-

sutulous (especially along veins); major veins usually 5 to 12 on a side, raised beneath, veinlet reticulum usually prominent beneath and sometimes prominulous; margins plane; petiole ca. 3–7 mm. long, usually distinctly channeled adaxially; stipules caducous (sometimes subpersistent), blunt to acuminate or acute-apiculate, mostly 4–8(–10) mm. long (occasionally only 2.5 mm. at first nodes of annual growth). Staminate flowers several per cluster; pedicels glabrous or hirsutulous, 2–5(–7) mm. long; sepals 4, subequal, the larger (inner) ones 0.8–1.5(–2) mm. long; disc thin, entire or minutely crenulate, (0.5–)1.0–1.8 mm. across; stamens 4, the filaments free or slightly united at base, 0.8–2 mm. long, the anthers ellipsoid, 0.4–1.4 mm. long. Pistillate flowers mostly 1 to 3 per axil; pedicels rather stout, subterete or angled, becoming (2–)3–8(–14) mm. long; sepals 4, subequal, oblong to ovate, the outer ones ca. 0.8–1.2 mm. long and broad, the inner ones 1.0–3.3 mm. long; disc rather thick, 1.5–2.7 mm. across; ovary usually of 3 carpels (90%), rarely of 2 (1.5%) or 4 (8.5%), the styles connate basally into a column 0.2–2 mm. high, with tips spreading, 0.8–1.5 mm. long, bifid. Capsules subglobose to oblate, scarcely to distinctly (but not deeply) 3-lobed, (5.5–)6–9(–11) mm. in diameter, endococci thin and papery; seeds with thin to thick sarcotesta, the endotesta smooth, plano-convex, (2–)2.3–3.2(–3.9) mm. long.

DISTRIBUTION. Deciduous forests or woodlands, sometimes in rainforests, most often in successional communities, from sea level to ca. 1000 meters elevation; western to eastern and southeastern Africa (MAP 4).

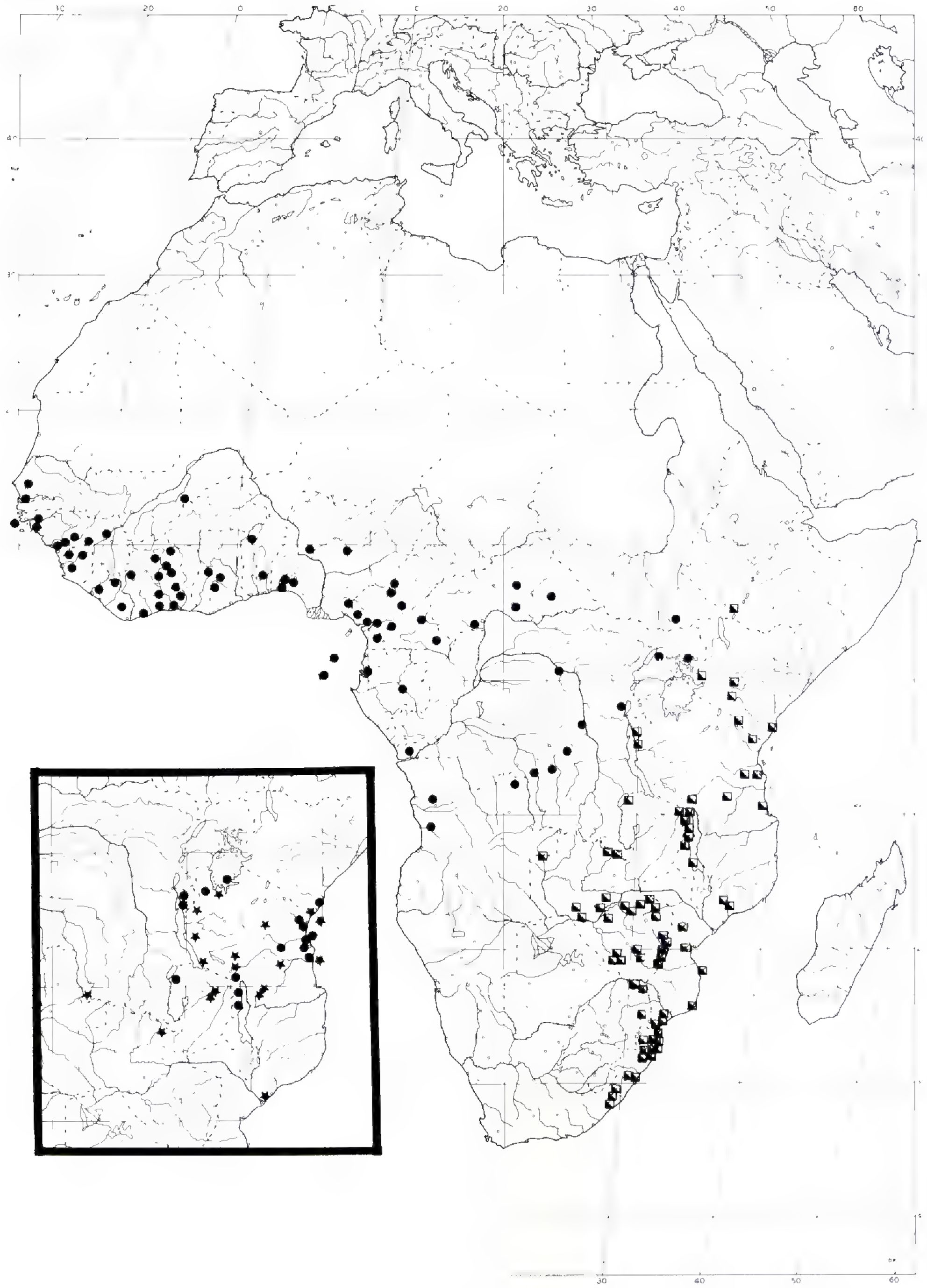
As noted by Radcliffe-Smith (1976), this widespread African species shows a great deal of variability. However, in contrast to *Margaritaria nobilis*, it exhibits a fairly clear differentiation into western and eastern populations that may be conveniently distinguished as subspecies. Although there is some overlap of characters, most specimens can be rather confidently assigned according to the characters detailed in the following key:

Stipules mostly 5–10 mm. long (at distal nodes); larger staminate sepals 1.1–1.5 mm. long; anthers mostly 0.4–0.7 mm. long; fruiting pedicels mostly 1.5–6 mm. long; stylar column 0.2–0.8(–1.1) mm. high; endotesta of seed mostly 2.5–3.5 mm. long; leaf blades mostly acute to acuminate at tip. . . . . subsp. 2a. *discoidea*.

Stipules mostly 2–5 mm. long (at distal nodes); larger staminate sepals 1.5–3 mm. long; anthers 0.8–1.4 mm. long; fruiting pedicels mostly 5–13 mm. long; stylar column 0.7–2 mm. high; endotesta of seed mostly 3.5–4.8 mm. long; leaf blades mostly obtuse to rounded at tip. . . . . subsp. 2b. *nitida*.

2a. **Margaritaria discoidea** subsp. **discoidea.** FIGURE 7.

Leaf blades mostly acute to acuminate at tip (occasionally obtuse); stipules usually caducous, generally acute to acuminate, (3–)5–8(–10) mm. long. Staminate flowers with sepals unequal, inner (larger) ones 1.1–1.5



MAP 4. Distribution of *Margaritaria* in Africa. Solid dots, *M. discoidea* subsp. *discoidea*; half-filled squares, *M. discoidea* subsp. *nitida*. Inset: *M. obovata* (solid dots; stars indicate localities cited by Radcliffe-Smith).

mm. long; disc (0.8–)1–1.3(–1.8) mm. across; anthers 0.4–0.7 mm. long. Pistillate flowers with pedicels becoming (1.5–)2.5–8(–13) mm. long; ovary of 3 carpels (88%), rarely of 2 (1.5%) or 4 (10.5%); stylar

column (0.2–)0.4–0.8(–1.1) mm. high; capsules (5.5–)6–8.5(–9.5) mm. across; endotesta of seed (2–)2.3–3.3(–3.5) mm. long.

DISTRIBUTION. Seasonal to evergreen rainforests, mostly below 1000 meters; Senegal to Angola, Zaire, and along the Rift Valley in eastern Africa (MAP 4); mainly in secondary vegetation (see Aubréville, 1959). Only a small portion of the specimens seen from West Africa are cited here.

REPRESENTATIVE SPECIMENS. **Angola:** Cuanza N., Cazengo, *Gossweiler 4692* (COI, NY, P). **Cameroon:** Bipindi, *Zenker 2890* (P, US). **Central African Empire:** Boukoko, *Tisserant 501* (P). **Ivory Coast:** Rasso, *Aubréville 560* (A, P). **Benin:** Cabolé, *Chevalier 23780* (P). **Gabon:** Libreville, *Klaine 1031* (A, P). **Gambia:** Albreda, *Heudelot 102* (P). **Ghana:** Asokroa, Kumasi, *Darko 595* (MO). **Guinea:** entre Konkouré et Timbo, *Chevalier 12499* (P). **Guinea-Bissau:** Fulacunda, *Espirito Santo 2162* (COI). **Liberia:** Barclayville, *Baldwin 11125* (NY). **Mali:** cercle de Kita, *Vuillet 247* (P). **Nigeria:** Ijebu, Oluasogo, *Ross 62* (MO, NY). **Senegal:** Thies-Diourbel, Kaolak, *Berhaut 1091* (P). **Sierra Leone:** Njala, *Deighton 1109* (MO). **Sao Tome & Principe:** Príncipe, *Espirito Santo 221* (COI); São Tomé, *Espirito Santo 3850* (COI). **Sudan:** Equatoria, Torit Rirt, *Andrews 1740* (K). **Togo:** Tamberma, *Kersting 343* (A). **Uganda:** Kipayo, *Dümmer 367* (MO, US); Teso, Serere, *Chandler 1063* (PRE). **Zaire.** EQUATEUR: Lukolela, *Chapin 598* (US). KIVU: Kalehe, *Pierlot 729* (BR), *Troupin 12520, 12595* (BR); Lueki, *Donie 2093* (MO). ORIENTALE: Isangi, *Léonard 1391* (MO).

Margaritaria discoidea subsp. *discoidea* is very similar morphologically both to the American *M. nobilis* and to the oriental *M. indica*. It appears closer to the American taxon because of the smooth endotesta of the seed and the tendency to have 4-carpellate fruits. However, no collections of *M. discoidea* subsp. *discoidea* having only 4 carpels have been seen; 65% of the collections have only 3 (or 2 and 3) carpels, and although 34% of the collections have both 3 and 4 carpels, the 4-carpellate fruits are always a small minority (TABLES 1, 2). Plants of *M. nobilis* from Mexico and Central America come closest to this condition, but 4-carpellate fruits there are nearly always in the majority. This difference in distribution of carpel number suggests to me that the American and African plants are best assigned to two different species. Staminate specimens of the three taxa are difficult or sometimes impossible to distinguish, and one could argue that the three taxa should be treated as a single circumtropical polymorphic species. However, the eastern African populations here accepted as a subspecies of *M. discoidea* would be difficult to accommodate in such a classification, and our knowledge of the populations still appears inadequate to justify such extreme lumping.

2b. **Margaritaria discoidea** subsp. **nitida** (Pax) Webster, comb. et stat. nov. *Flueggea nitida* Pax, Bot. Jahrb. 19: 76. 1894. TYPE: Mozambique, Quilimane, *Stuhlmann 559* (*n.v.*; the original specimen at B presumably having been destroyed, I hereby designate as neotype the following collection: Mozambique, entre Nampevo e Mugeba, *Grandvaux Barbosa & Carvalho 2950* (K)).

Flueggea fagifolia Pax, Pflanzenw. Ost.-Afr. C, 236. 1895. TYPE: Tanzania, Kilimanjaro, *Volkens 1737* (K, lectotype).

Phyllanthus ? amapondensis Sim, Forests Forest Fl. Colony Cape Good Hope, 325. *t. 141, fig. 2.* 1907. TYPE: South Africa, Pondoland, Egossa Forest, *Sim 2608* (PRE, holotype).

Leaf blades mostly obtuse or subacute at tip, occasionally rounded or emarginate, rarely acuminate; stipules caducous or persistent, 2.5–5(–6) mm. long; inner (larger) staminate sepals (1.5–)1.8–2.5(–3) mm. long; staminate disc 0.5–1.1(–1.5) mm. across; anthers 0.8–1.4 mm. long; pistillate flowers with pedicels becoming (5–)6–10(–13) mm. long; ovary nearly always of 3 carpels (97%), very rarely of 2 or 4 (1.5% each), styles usually connate ½ to ¾ their lengths, the column 0.8–2 mm. high; capsules (9–)10–13 mm. in diameter; endotesta of seeds (3.5–)3.8–4.8 mm. long.

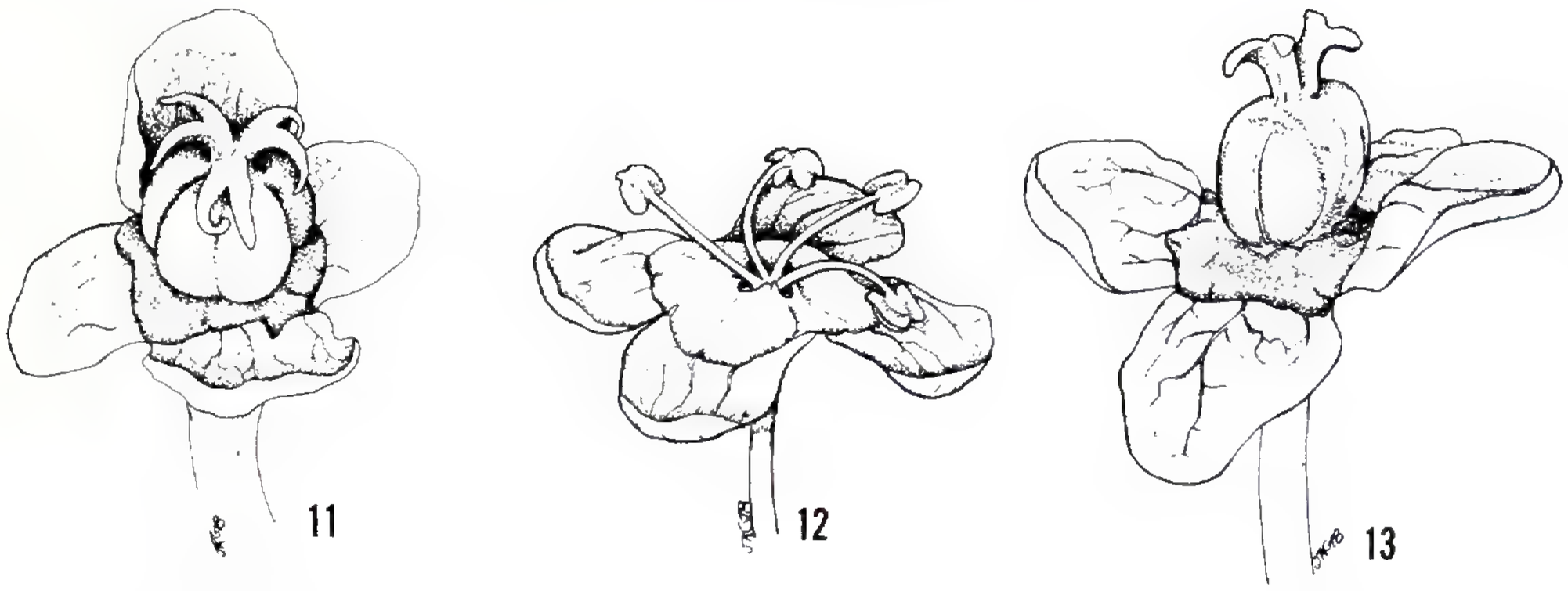
DISTRIBUTION. Burundi and southwestern Ethiopia south to Rhodesia and South Africa (MAP 4); a large number of additional specimens are cited by Radcliffe-Smith (1976).

SPECIMENS EXAMINED. **Burundi:** Bururi, Kigwena, *Reekmans 3192* (PRE). **Ethiopia:** S. Sidamo, *Chaffey 132* (K). **Kenya.** CENTRAL: Nyeri, *Porter 933* (PRE). COAST: Kilifi, Sokoke, *Gisau SOK6* (PRE). NAIROBI: Nairobi, National Museum grounds, *Mwangangi 1768* (MO); Coryndon Museum grounds, *Williams 427* (K, PRE); Chiromo, *Agnew 7784* (MO), *Gillett 16593* (MO). WESTERN: Kakamega Forest, *Drummond & Hemsley 4797* (PRE, K). **Malawi.** CENTRAL: Salima, *Robson & Steele 1613* (PRE). NORTHERN: Chendo River, between Fort Hill and Chisenga, *Robson & Fanshawe 556* (PRE); Chitipa Distr., Kaseye, *Pawek 13359* (DAV); Karonga Distr., 5 mi. W. of Karonga, *Pawek 12112* (DAV); Mzimba Distr., 1¼ mi. SE. of Mzambazi Mission, *Pawek 11960* (DAV); Nkhata Bay Distr., road to Nkhata Bay from Mzuzu, *Pawek 12046* (DAV). **Mozambique.** GAZA: Macia, S. Martinho do Bilene, *Grandvaux Barbosa 8338* (COI); entre Chissano e Licilo, *Grandvaux Barbosa & Lemos 7970* (COI, K). INHAMBANE: Sul do Save, Nhacoongo, *Macedo & Balsinhas 1101* (PRE); Bazaruto Is., Pont Estone, *Mogg 28639* (PRE). MAPUTO: Muntanhane, *Balsinhas 237* (PRE); Lourenço Marques, *Borle 174* (PRE), *Hornby 2880* (PRE); Bela Vista, Floresta do Licauti, *Lemos & Balsinhas 259* (PRE); Vila Luiza, *Grandvaux Barbosa & Lemos 7907* (COI). MANICA E SOFALA: Buzi, Reserva Florestal do Mucheve, *Fidalgo de Carvalho 703* (PRE); Mt. Gorongosa, *Muller & Gordon 1396* (PRE). ZAMBEZIA: entre Nampevo e Mugeba, *Grandvaux Barbosa & Carvalho 2590* (K); Quelimane, Lugela-Moruba, Namagoa Plantation, *Faulkner 314* (K). **Rhodesia.** MANICALAND. Chipinga Distr.: Makosa hills, *Phelps 197* (PRE); Mwangazi Gap, *Farrell 163* (PRE); Dotts Drift, *Goodier 664* (PRE). Melsetter Distr.: Umvumuvumu River, *Armitage 158* (PRE); Lusitu Valley, Ngorima Reserve, *Wgoni 65* (MO). Stapleford Distr.: Mt. Wuza, *Goldsmith 26749* (PRE). Umtali Distr.: 25 mi. S. of Umtali, *Drummond 5049* (PRE); Christmas Pass, *Gilliland 1260* (PRE); Umtali Golf Course, *Chase 5150* (MO). MASHONALAND NORTH. Darwin Distr.: Chiswiti Reserve, *Phipps 2358* (PRE). Urungwe Distr.: Deve, *Goodier 459* (PRE); Msukwe River, *Wild 4160* (MO, PRE); Urungwe, *Lovemore 311* (MO, PRE). Lomagundi Distr.: Mangula, *Jacobsen 2498, 2971* (PRE). MASHONALAND SOUTH. Mrewa Distr.: Shawnoye River bridge, *Moll 592* (NY). MATABELELAND. Sebungwe Distr.: Kariangwe Hill, *Lovemore 175* (NY, PRE); Suainga, *Lovemore*

487 (PRE); Victoria Falls, *Wilson s.n.* (A). Matopos Distr.: Moth Shrine Koppie, *Plowe 1320* (NY); Besna Kobila, *Miller 1991* (MO, PRE); Quaringa, *Miller 2522, 3295* (PRE). VICTORIA. Chibi Distr.: Madzivire Dip, *Moll 385* (NY). **South Africa.** CAPE OF GOOD HOPE: Pondoland, Egossa Forest, *Sim 2608, 19618* (PRE). NATAL: Hlabisa, *Ward 2677, 2819* (PRE); Hluhluwe Game Reserve, *Codd 9627* (PRE); *Fakude 20* (PRE), *Pegel 102* (PRE); Mbizatsheni, *Ward 6058* (PRE); Wall's farm, *Gerstner 5006* (PRE). Ingwavuma Distr.: Maputa, *de Winter & Vahrmeijer 8601* (PRE), 16 mi. from Ndumu toward Ingwavuma, *Moll 4353* (PRE); confluence Pongola/Usutu, *Dutton s.n.* (PRE); Ndumu Game Reserve, *Strey & Moll 3751* (NY), *Tinley 406* (PRE), *Ward 2474* (PRE). New Hanover Distr.: Benvie, Karkloff, *Moll 3374* (PRE). Port Shepstone Distr.: Amanzimtoti, *Ward 6038* (PRE); Isipingo Flats, *Ward 6715* (PRE). Westville Distr.: Mologodhlo Valley, *Haycroft s.n.* (PRE). TRANSVAAL: near Lothian, *Chief Forestry Res. Officer 81* (PRE); Kruger National Park, Dzundweni Hill, 12 mi. SE. of Punda Maria, *Codd & Dyer 4591* (PRE), Zoutpansberg, *Codd & Dyer 4545* (PRE). SWAZILAND: Hlatikuhu Forest, *Forestry Herb. 5324* (PRE). **Tanzania.** KIGOMA: Kigoma, *Humbert 7185* (P). KILIMANJARO: Am Himo, *Volkens 1737* (K). MBEYA: Kyimbila, *Stolz 1744 (ex. p.), 1770* (A, MO). MOROGORO: Vigude, Kilosa Distr., *Semsei 5987* (MO); Ulugurus, *Bruce s.n.* (P); Mahenge, *Schlieben 1467* (P). MTAWARA: Lindi, *Schlieben 5460* (M, P, S). TANGA: Lushoto Distr., Ndola Reserve, *Semsei 2966* (PRE), Lushoto-Gare track, *Semsei 3190* (PRE). **Uganda.** BUNYORO: Foweira, *Bagshawe 1572* (US). **Zambia.** LUAPULA: Kafulwe Mission, Lake Mweru, *White 3600* (MO). NORTHWESTERN: Balovale Distr., Chavuma, *White 3490* (MO, PRE). SOUTHERN: Mazabuka Distr., Kanchale, *White 6326* (NY); Victoria Falls, *Burtt Davy 601* (PRE); Siburu Forest, Sekute Chieftancy, *Bainbridge 705* (NY); Mapanza, Chomo, *Robinson 2506* (PRE). WESTERN: Zimbabwe, Chipopo Falls, *Mullin 89/51* (NY); Ndola, *Fanshawe F731* (BR).

The status of the eastern African populations of *Margaritaria discoidea* remains controversial. Radcliffe-Smith (1976), while recognizing *M. obovata* at varietal rank, grouped all other forms of eastern African *Margaritaria* in *M. discoidea*. However, although there are overlaps of measurement in most characters in the eastern and western African populations, I believe that they are modally distinctive enough to merit separation at the subspecific level. Specimens somewhat intermediate between subsps. *discoidea* and *nitida* are known from Sudan, Uganda, and Zaire. However, the sampling of collections from these areas is still not very good, so the position of the boundary line or zone between the two subspecies is not yet well defined.

3. **Margaritaria scandens** (Wright ex Griseb.) Webster, Jour. Arnold Arb. **38**: 66. 1957. *Cicca antillana* var. α *glaucescens* Griseb. Mem. Am. Acad. II. **8**: 157. 1860. *Phyllanthus antillanus* ε *glaucescens* (Griseb.) Mueller-Arg. Linnaea **32**: 51. 1863. *Cicca scandens* Wright ex Griseb. Nachr. Ges. Wiss. Göttingen **1865**: 165. 1865. *Phyllanthus scandens* (Griseb.) Mueller-Arg. in DC. Prodr. **15**(2): 415. 1866. *Diasperus scandens* (Griseb.) O. Kuntze, Rev. Gen. Pl. **2**: 601. 1891. TYPE: Cuba, Oriente, Monteverde, *Wright 1437* (GOET, holotype). FIGURES 1, 11.



FIGURES 11–13. Flowers of *Margaritaria*: 11, *M. scandens* (*Brace 168*), pistillate; 12, *M. hotteana* (*Ekman H8909*), staminate; 13, *M. hotteana* (*Ekman H8919*), pistillate; all × 7.5.

Phyllanthus bahamensis Urban, Symb. Antill. 3: 289. 1902. *Margaritaria bahamensis* (Urban) Britton & Millsp. Bahama Fl. 220. 1920. LECTOTYPE: Andros, Red Bays, *Northrop s.n.* (GH, lectotype).

Straggling or somewhat scandent shrub or small tree up to 5 meters high; branches scabridulous when young, reddish and becoming more or less smooth in age; foliage evergreen, or partly deciduous. Leaf blades firmly chartaceous, elliptic to obovate or lanceolate, mostly 3–7 cm. long, 1.5–2.5 cm. broad, obtuse or bluntly pointed at tip, cuneate at base, decurrent on petiole, often glaucous beneath; major veins ca. 7 to 12 on a side, not conspicuous above, beneath raised, the veinlet reticulum often prominent but not prominulous; margins plane or recurved; petioles 3–7 mm. long, distinctly adaxially channeled; stipules ovate-lanceolate, scarious, becoming more or less indurate and subpersistent, cordate, acuminate, (1–)1.5–2.5(–3.5) mm. long. Staminate flowers few to several per axil (rarely solitary); pedicels stout, 2–5 mm. long; sepals biseriate, ovate to elliptic, the outer pair 1–1.7 mm. long, 1–1.4 mm. broad, the inner pair 1.4–2.1 mm. long, 1.2–1.9 mm. broad; disc thickish, 1.2–2.1 mm. across; stamens 4, free, the filaments becoming 0.5–1.3(–2) mm. long, the anthers elliptic, 0.5–0.7(–1) mm. long. Pistillate flowers 1 to 3 per axil; pedicels subterete, (1.5–)3–7(–9) mm. long; sepals 4, biseriate, subequal, 1.5–2.3 mm. long and broad; disc thick, 2.3–3 mm. across; ovary of 3 (less commonly 4) carpels, the styles free, spreading, 1–1.5 mm. long, bifid. Fruits oblate, shallowly 3-lobed, 7–10 mm. in diameter, irregularly dehiscent, endococci papery; seeds with thick blue-green sarcotesta, the endotesta smooth, plano-convex, 2.7–4.2 mm. long, 2.4–3.5 mm. broad.

DISTRIBUTION. Hammocks, pine forests, and evergreen forests; Bahamas and Cuba (MAP 2).

SPECIMENS EXAMINED. **Bahamas.** ANDROS. N. Andros: Mangrove Cay, *Brace 4867* (NY); Nicholllstown, *Correll & Evans 43929* (NY); Conch Sound, Strachan Hill, *Brace 6924* (NY); road to Conch Sound, *Brace 6784* (NY); road to Louisa Coppice, *Brace 6270* (A); 2 mi. NW. of Love Hill, *Hill 3027, 3035* (NY); Mastic

Point, *Brace 6983* (NY); Crow Hill, *Small & Carter 8720* (NY); Smith Hill, *Small & Carter 8678* (NY); 1 mi. N. of Smith's Hill, *Correll 43522* (NY). ELEUTHERA: Spanish Wells, *Coker 328* (NY); The Bluff, *Russell 1* (DAV). GREAT ABACO: road to Hole-in-the-wall, 6 mi. below intersection with Sandy Point Rd., *Correll & Meyer 44559* (NY); California Road, *Brace 2037* (NY). GREAT EXUMA: Stuart Manor, *Correll 44107* (NY). NEW PROVIDENCE: Nassau, *Brace 3906*, (NY), *Curtiss 183* (A, NY); Farringdon Road, *E. G. Britton 3043* (NY); Fort Charlotte Rd., *Brace 7147* (NY); Maiden-hair Coppice, *Wilson 8394* (NY), *E. G. Britton 3435* (NY); between Love and Gambier, *Degener 19140* (A, NY); Waterloo, *Britton & Brace 741* (NY), *Degener 19139* (A, NY); Blue Hills, between Lake Cunningham and Lake Killarney, *Webster, Samuel, & Williams 10514* (DAV). **Cuba.** LA HABANA: Isle of Pines, *Jennings 678* (NY). ORIENTE: Mt. Libano, 1860, *Wright s.n.* (GOET); La Perla, Monteverde, *Wright 1437* (GOET, holotype; BR, F, G, GH, NY, S, W, isotypes).

Several barren specimens from Oriente Province, Cuba, are distinctive in their thick, revolute leaves with a thick, waxy, glaucous bloom beneath: Lomas de Duaba, near Baracoa, *Ekman 4236* (S); Moa, La Brena, *León & Clemente 23339* (MICH); Toa, charrascos de Pena Prieta, *Alain 3481* (DAV); Pico Galano, Toa, *Alain 3761* (DAV). These may represent a form of *Margaritaria scandens* or perhaps an undescribed species.

There is still some uncertainty as to the application of the name *Margaritaria scandens* because the species has not been re-collected in Cuba since Wright's original gatherings. From these incomplete specimens, it is difficult to be absolutely certain that the Bahama plants are conspecific. However, until the Cuban population can be restudied, it seems best to treat *M. bahamensis* as a synonym of *M. scandens*. Unfortunately, I had earlier (Jour. Arnold Arb. 39: 208. 1958) mistakenly treated *M. bahamensis* as a synonym of *M. tetracocca* rather than of *M. scandens*.

4. **Margaritaria tetracocca** (Baillon) Webster, Jour. Arnold Arb. **38**: 66. 1957. *Wurtzia tetracocca* Baillon, Adansonia I. **1**: 187. 1861. TYPE: Cuba, Oriente, *Wright 583* (G, holotype; GOET, isotype).

Cicca antillana var. *β virens* Griseb. Mem. Am. Acad. II. **8**: 158. 1860. *Phyllanthus antillanus β virens* (Griseb.) Mueller-Arg. Linnaea **32**: 51. 1863. *Cicca virens* (Griseb.) Wright ex Griseb. Nachr. Ges. Wiss. Göttingen **1865**: 166. 1865. *Phyllanthus virens* (Griseb.) Mueller-Arg. in DC. Prodr. **15**(*2*): 415. 1866. *Diasperus virens* (Griseb.) O. Kuntze, Rev. Gen. Pl. **2**: 601. 1891. TYPE: Cuba, Oriente, *Wright 584* (GOET, lectotype; G, GH, S, isotypes).

Shrub to 3 meters high; branches subterete, scabridulous at least when young; foliage evergreen. Leaf blades firmly chartaceous, elliptic or oblong, 3–9 cm. long, 1.5–3.5 cm. broad, obtuse or bluntly pointed at tip, cuneate at base, decurrent on petiole, shining above, paler but not glaucous beneath; major veins ca. 7 to 12 on a side, inconspicuous above, raised beneath, veinlet reticulum rather conspicuous beneath but not very prominulous; margins more or less revolute; petioles 4–7 mm. long, adaxially channeled; stipules ovate, basally auriculate, acuminate, hardly scarious, becoming dark and indurate, 1.5–2.7 mm. long. Staminate flow-

ers several per cluster; pedicels stout, 2–3 mm. long; sepals biseriate, 1.8–2.5 mm. long, the inner ones ca. 1.7–2.5 mm. broad (outer ones narrower); disc obsolete; stamens 4, free, the filaments 0.5–0.8 mm. long, the anthers oblong, 1–1.3 mm. long. Pistillate flowers solitary; pedicels subterete, scabridulous, 2.5–5.5 mm. long; sepals 4, biseriate, subequal, ovate, 1.5–2.3 mm. long, 1.2–2.1 mm. broad; disc rather thin, 1.5–1.8 mm. across; ovary of 4 (rarely 3) carpels, apically indented, the styles 1.5–2 mm. long, connate basally into a column 0.4–0.7 mm. high, bifid. Fruits oblate, shallowly to rather deeply 4-lobed, apically depressed, 9–10 mm. in diameter; seeds apparently with a thin sarcotesta, the endotesta smooth, plano-convex, 2.7–3.2 mm. long, 2.7–2.9 mm. broad.

DISTRIBUTION. Endemic to montane forests; Cuba and Hispaniola (MAP 2).

SPECIMENS EXAMINED. **Cuba.** ORIENTE: "Cuba Orientali," 1856–57, *Wright 583* (G, GOET); Monteverde, 1859–60, *Wright 584* (G, GH, GOET); Pinal de Santa Ana, *Eggers 5026* (A). PINAR DEL RÍO: Pan de Guajaibón, *Acuña & Alain 18549, 18550* (HAC), *Alain & Acuña 2999* (US). **Haiti.** SUD: Massif de la Hotte, central group, St. Louis du Sud, Bonnet-Carré, ca. 1150 m. alt., *Ekman H9234* (S).

Margaritaria tetracocca is still a poorly known species, but it appears to be quite distinct from the much more common and more widely distributed *M. scandens*. The absence of a glaucous bloom on the underside of the leaves in *M. tetracocca* is characteristic, although some forms of *M. scandens* also lack this character. However, the stipules of *M. tetracocca* are consistently different in their auriculate base and indurate texture, so even barren specimens can be distinguished from *M. scandens*.

The specimens from Pinar del Río and from Haiti are somewhat divergent from the type collection, and the Haitian plant in particular may — when better known — prove to be subspecifically or even specifically distinct.

5. **Margaritaria hotteana** (Urban & Ekman) Webster, Jour. Arnold Arb. **38**: 66. 1957. *Phyllanthus hotteanus* Urban & Ekman, Arkiv Bot. **22A**(8): 61. 1929. TYPE: Haiti, *Ekman H8909* (S, holotype; G, isotype). FIGURES 12, 13.

Low, straggling shrub; twigs slender, scabridulous when young, lenticellate in age, some twig tips becoming spinescent. Leaf blades thinly chartaceous, elliptic or oblong to obovate, 1–2.5 cm. long, 0.4–0.8 cm. broad, obtuse or rounded (and sometimes minutely apiculate) at tip, cuneate at base, decurrent on petiole, slightly shiny above, green and paler beneath; veins obscure above, midrib prominently raised beneath, major veins 5 to 10 on a side, veinlet reticulum fine and not prominulous; margins plane or slightly recurved; petioles 1–3 mm. long, adaxially channeled; stipules lanceolate, scarious, pale, mostly deciduous, 0.7–2 mm. long. Staminate flowers 1 to 3 per axil; pedicels slender, 3–6 mm. long;

sepals biseriate, oblong to obovate, 1.3–2 mm. long, 1.0–1.7 mm. broad (outer ones narrower); disc 4-angled, minutely scabridulous, 1.5–2.2 mm. across; stamens 4, free, the filaments 1–1.5 mm. long, the anthers elliptic, 0.5–0.6 mm. long. Pistillate flowers solitary; pedicels subterete, 2–3 mm. long; sepals 4, biseriate, the outer ones ovate, the inner ones oblong-elliptic, 1.7–1.8 mm. long, 1.3–1.7 mm. broad; disc 4-lobed, ca. 1.5 mm. across; ovary of 2 carpels, the styles nearly free, spreading, somewhat dilated, bifid, 0.7–1 mm. long. Fruits not seen.

DISTRIBUTION. Endemic to forests on limestone; southern Haiti (MAP 2).

SPECIMENS EXAMINED. **Haiti.** SUD: Massif de la Hotte, Morne Rochelois, Miragoane, towards Charlier, 14 Aug. 1927, *Ekman H8909* (G, S); Grande-Caïmite, Source-Fantasque, 20 Aug. 1927, *Ekman H8919* (S); St.-Michel de l'Atalaye, Morne la Cidre, limestone crags, ca. 750 m., *Ekman H8364* (S).

As noted by Ekman (ms.), the habit of this species is very similar to that of *Flueggea acidoton*; however, despite the lack of fruits, the floral disc clearly indicates that the plant belongs to *Margaritaria*. The scabridulous twigs suggest an affinity to *M. scandens* and *M. tetracocca*, but it differs from those species in its slender, spinescent branch tips, smaller leaves, and bicarpellate ovary.

6. **Margaritaria luzoniensis** (Merr.) Airy Shaw, Kew Bull. 20: 387. 1966.
Phyllanthus luzoniensis Merr. Philip. Jour. Sci. Bot. 7: 404. 1912.
Prosorus luzoniensis (Merr.) Airy Shaw, Kew Bull. 16: 343. 1963.
TYPE: Luzon, Pampanga Prov., *Curran FB 17698* (A, lectotype). FIGURE 4.

Tree to ca. 10 meters high; foliage deciduous; twigs subterete, reddish-hirsutulous when young, glabrate in age, lenticellate. Leaf blades thinly chartaceous, elliptic to obovate, (2–)2.5–5 cm. long, 1–2.5 cm. broad, obtuse to rounded at apex, cuneate at base, slightly decurrent on the petiole above, beneath paler and hirsutulous when young (glabrate in age); veins (5 to 8 on a side) and veinlets anastomosing in a prominent reticulum, prominulous especially beneath; margins plane; petiole mostly 2–4 mm. long, slightly laterally flanged but not adaxially channeled; stipules caducous, brownish-scarious, lanceolate, hirtellous, ca. 1–1.5 mm. long. Staminate flowers several per axillary cluster; pedicels 4–6(–8) mm. long, hirsutulous; sepals biseriate, hirsutulous, the outer ones ovate, 1.3–1.6 mm. long, 0.8–1 mm. broad, the inner ones obovate, 1.6–2 mm. long, 1.1–1.5 mm. broad; disc thin, 0.5–0.9 mm. across; stamens 4, the filaments free, becoming 0.8–1.5 mm. long, the anthers elliptic, 0.6–0.7 mm. long. Pistillate flowers solitary; pedicels subterete, hirsutulous, 8–17 mm. long; calyx and ovary not seen in flower. Fruits subglobose, 6–10 mm. in diameter, 3-carpellate, columella more or less persistent; seeds with distinct dark sarcotesta, the endotesta smooth, plano-convex, 4.1–5.1 mm. long, 2.6–3.1 mm. broad.

DISTRIBUTION. Dry forests, lower elevations; endemic to Luzon.

SPECIMENS EXAMINED. **Philippines. Luzon.** BATAAN: Corregidor Is., *Curran FB 13225* (A, US). NUEVA ECIJA: Mt. Umingan, *Ramos & Edaño BS 26282* (US). PAMPANGA: Mt. Arayat, *Curran FB 17698* (A, lectotype). PANGASINAN: Umingan, *Otanes BS 17834* (A, US).

Airy Shaw (1971) has questioned the distinctness of *Margaritaria luzoniensis* from *M. indica* on the basis of certain specimens of the latter that have small fruits. Actually, in the one collection (*Ramos & Edaño BS 26282*) of *M. luzoniensis* with mature fruit, the seeds are larger than those of *M. indica*. A better seed character is provided by the surface of the endotesta, which is smooth in *M. luzoniensis* and at least somewhat (often pronouncedly) rugose in *M. indica*. The small, blunt leaves with non-channeled petiole (FIGURE 4) and reddish pubescence of *M. luzoniensis* make it easily recognizable even in the barren condition, and there appears to be no reason not to give it specific rank.

7. **Margaritaria indica** (Dalz.) Airy Shaw, Kew Bull. **20**: 387. 1966. *Prosorus indicus* Dalz. Jour. Bot. Kew Misc. **4**: 345. 1852. *Phyllanthus indicus* (Dalz.) Mueller-Arg. Linnaea **32**: 52. 1863; in DC. Prodr. **15**(2): 417. 1866. TYPE: India, Deccan, *Dalzell s.n.* (K).

Phyllanthus stocksii Mueller-Arg. Linnaea **32**: 151. 1863. TYPE: India, *Stocks & Law s.n.* (G).

Calococcus sundaicus Kurz ex Teijsm. & Binn. Nat. Tijdschr. Nederl. Ind. **27**: 48. 1864. *Phyllanthus sundaicus* (Kurz) Mueller-Arg. in DC. Prodr. **15**(2): 1272. 1866. *Diasperus sundaicus* (Kurz) O. Kuntze, Rev. Gen. Pl. **2**: 599. 1891. TYPE: "in freto sundaico," *Teijsmann s.n.* (holotype, presumably BO, *n.v.*; G, isotype).

Phyllanthus indicus f. *vestita* J. J. Sm. Bijdr. Booms. Java **12**: 87. 1910. TYPE: Java, G. Watoedodol, *Koorders s.n.* (BO, *n.v.*).

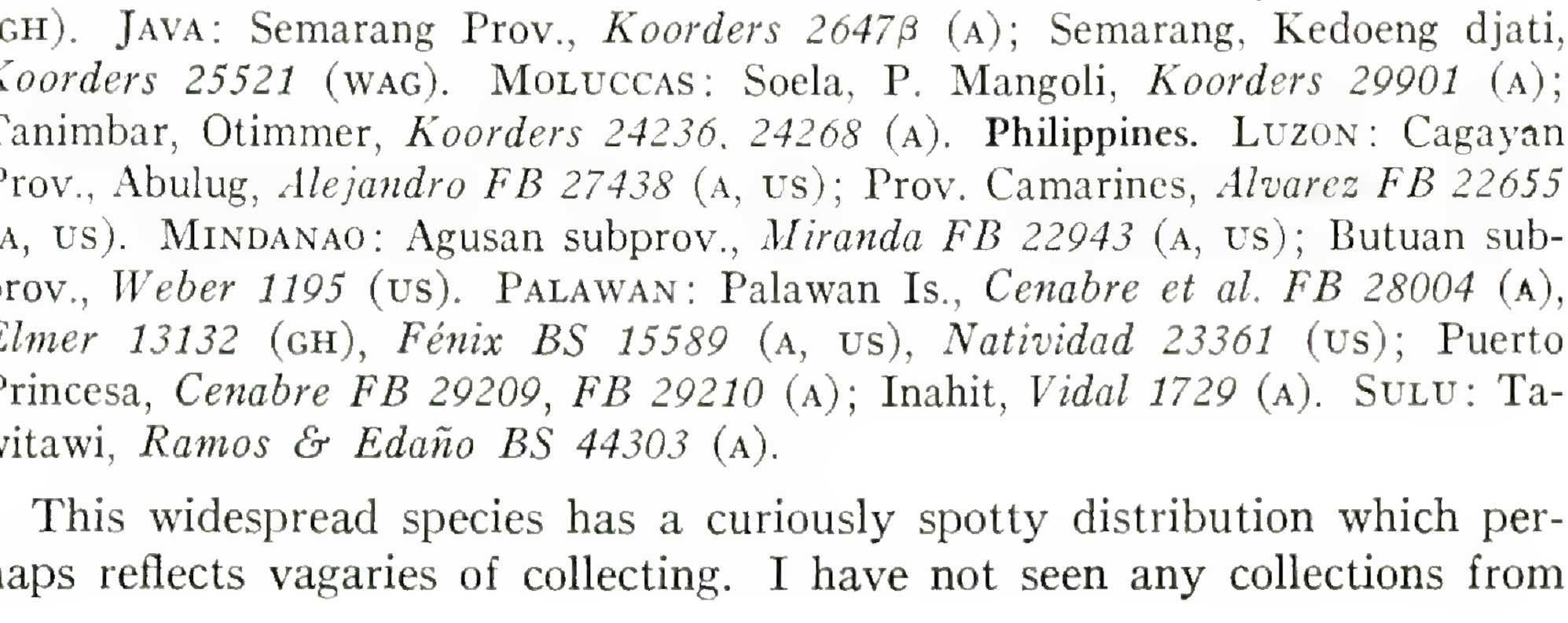
Glabrous trees up to 25 meters high; foliage deciduous; twigs brownish, more or less prominently lenticellate, subcompressed. Leaf blades thinly chartaceous, elliptic to oblong-lanceolate, ca. 5–13 cm. long, 3–6 cm. broad, distinctly and sometimes abruptly acuminate at tip, cuneate to rounded at base and more or less adaxially decurrent on the petiole, usually paler beneath; veins (mostly 8 to 12 on a side) and veinlets prominulous beneath; margins plane or incurved; petiole mostly 5–8 mm. long, adaxially channeled; stipules caducous, brownish-scarious, lanceolate, more or less acuminate, 2.5–4.5 mm. long. Staminate flowers several per axillary cluster; pedicels ca. 4–6 mm. long; sepals 4, biseriate, the outer ones ovate, 1–1.5 mm. long, 0.6–1 mm. broad, the inner ones obovate, 1.3–1.8 mm. long, 1–1.5 mm. broad; disc adnate, smooth or somewhat rugulose, 0.6–1.5 mm. across; stamens 4, the filaments free, becoming 0.7–1.5 mm. long, the anthers elliptic or oblong, 0.6–0.9 mm. long. Pistillate flowers 1 to 3 per axil; pedicels subterete, 8–21 mm. long; sepals 4, biseriate, ovate to oblong, entire, ca. 1.5–2 mm. long; disc entire, adnate, 1.8–2.8 mm. across; ovary almost always of 3 (very rarely 4) car-

pels, the styles free or basally connate, spreading, ca. 1.5–2 mm. long, bifid. Fruits subglobose, scarcely lobed, irregularly dehiscent, (7–)9–12 mm. in diameter, endococci papery; seeds with rather thickish, bluish sarcotesta, the endotesta usually distinctly rugose or furrowed on back, plano-convex, (3.5–)3.9–4.8 mm. long, (2.7–)3–3.7(–4.2) mm. broad.

DISTRIBUTION. Mostly in lowland (below 1000 meters) deciduous or semi-evergreen monsoon forests; India and Ceylon to Thailand, Formosa, Indochina, the Philippines, Indonesia, and Australia (MAP 5). Additional localities in Java are cited by J. J. Smith (1910), and other oriental localities are given by Airy Shaw (1963, 1976).

SPECIMENS EXAMINED. **India.** Kanara, *Talbot 1173* (K). MYSORE: 20 mi. S. of Belgaum, *Ritchie 1343* (GH); Hassan Distr., Yettinahalla, *Saldanha 13263* (K), *Nicolson et al. HFP 80* (MO); Shiradi ghat, *Saldanha 13140* (MO). **Sri Lanka:** Nannapurawa, Moneragala Distr., *Waas 663* (MO). **Burma:** Bassein Distr., Chaungtha Is., *Lace 3034* (K). **Thailand:** Chaiyaphum Distr., *van Beusekom et al. 4207* (K, MO); Lampang, Wang Fen, *Winit 1957* (K); Saraburi, Phu Kae, *Chamroerngsri 2* (K). **Vietnam.** TONKIN: Dam-ha, *Tsang 30219* (A, S); Ha-coi, *Tsang 29583* (A, S). **Malaysia.** PAHANG: Pulau Chibeh, P. Tioman, *Corner SFN 29829* (A). **Indonesia.** SUMATRA: without locality, *Forbes 2733* (GH). JAVA: Semarang Prov., *Koorders 2647β* (A); Semarang, Kedoeng djati, *Koorders 25521* (WAG). MOLUCCAS: Soela, P. Mangoli, *Koorders 29901* (A); Tanimbar, Otimmer, *Koorders 24236, 24268* (A). **Philippines.** LUZON: Cagayan Prov., Abulug, *Alejandro FB 27438* (A, US); Prov. Camarines, *Alvarez FB 22655* (A, US). MINDANAO: Agusan subprov., *Miranda FB 22943* (A, US); Butuan subprov., *Weber 1195* (US). PALAWAN: Palawan Is., *Cenabre et al. FB 28004* (A), *Elmer 13132* (GH), *Fénix BS 15589* (A, US), *Natividad 23361* (US); Puerto Princesa, *Cenabre FB 29209, FB 29210* (A); Inahit, *Vidal 1729* (A). SULU: Tawitawi, *Ramos & Edaño BS 44303* (A).

This widespread species has a curiously spotty distribution which perhaps reflects vagaries of collecting. I have not seen any collections from



MAP 5. Distribution of *Margaritaria indica* (solid dots), *M. dubium-traceyi* (open circles), and *M. anomala* (stars; more detailed distribution within Madagascar given in MAP 6).

China, although Tsang's collections from Viet Nam were made only a few miles from the border. Since it has been found in Taiwan (Keng, 1951), it may be expected in Hainan. Keng (1955) suggested that the plant is probably introduced in Taiwan, but this seems rather improbable in view of the fact that it is scarcely, if ever, deliberately cultivated anywhere. Airy Shaw (1963) reported the species from China (Kwantung), Borneo (Sarawak), and the Kangean Islands; and more recently (1971) he has extended the range to New Guinea.

Margaritaria indica is very closely related to the African *M. discoidea*, from which it cannot be surely distinguished except by virtue of the rugose endotesta of the seed. Airy Shaw (1971) notes that some Philippine specimens suggest possible intergradation with *M. luzoniensis*; however, the available sampling of specimens is still far too scanty, and field investigations will be necessary to come to any conclusions about changes in taxonomic status.

8. **Margaritaria cyanosperma** (Gaertner) Airy Shaw, Kew Bull. 20: 387. 1966. *Croton ? cyanospermus* Gaertner, Fruct. Semin. Pl. 2: 120. *pl. 107*. 1791. *Prosorus gaertneri* Thwaites, London Jour. Bot. 8: 272. 1856. *Prosorus cyanospermus* (Gaertner) Thwaites, Enum. Pl. Zeyl. 281. 1861. *Phyllanthus cyanospermus* (Gaertner) Mueller-Arg. Linnaea 32: 51. 1863; in DC. Prodr. 15(2): 416. 1866. TYPE, *n.v.*; neotype: Ceylon, *Thwaites CP 2601* (PDA, holotype, *n.v.*).

Zygospermum zeylanicum Thwaites ex Baillon, Étude Gén. Euphorb. 620. *pl. 27, fig. 11*. 1858. TYPE: Ceylon, *Thwaites* (P, *n.v.*).

Glabrous tree; foliage deciduous; twigs brownish. Leaf blades thinly chartaceous, elliptic, ca. 5–9 cm. long, 2–4 cm. broad, cuspidate-acuminate at tip, cuneate at base; veins (ca. 5 to 10 on a side) and veinlets prominulous; margins plane; petioles 4–8 mm. long, adaxially channeled; stipules deciduous, lanceolate, scarious, acuminate, ca. 3–4 mm. long. Staminate flowers several per cluster; pedicels mostly 8–10 mm. long; sepals 4, biseriate, reticulate veined, the outer ones oblong, ca. 3.5–4 mm. long, 1.4–1.8 mm. broad, the inner ones obovate, 3.5–4 mm. long, 2.2–2.7 mm. broad; disc rather tenuous, 0.8–1 mm. across; stamens 4, the filaments free, 0.5–0.7 mm. long, the anthers linear-oblong, 1.8–2 mm. long. Pistillate flowers solitary; pedicels slender, 15–17 mm. long, 2.2–3 mm. broad; disc adnate and very tenuous (nearly obsolete), ca. 2 mm. across; ovary of 3 carpels, the styles free or nearly so, ca. 0.9–1.3 mm. long, bipartite, tips rather slender. Fruits subglobose, ca. 9–10 mm. in diameter, the columella persistent, slender, 6–6.5 mm. long, the endococci papery; seeds with thickish, dark sarcotesta, the endotesta deeply rugose-furrowed, plano-convex, (3.2–)3.5–4.5 mm. long, 3.5–4.0 mm. broad.

DISTRIBUTION. Endemic to Sri Lanka.

SPECIMENS EXAMINED. **Sri Lanka:** without specific locality, *Thwaites CP 2155*

(A), *CP 2601* (GH, L). Thwaites (1856) cited Ambagamowa and Ratnapoor districts, but the species seems not to have been re-collected in recent times.

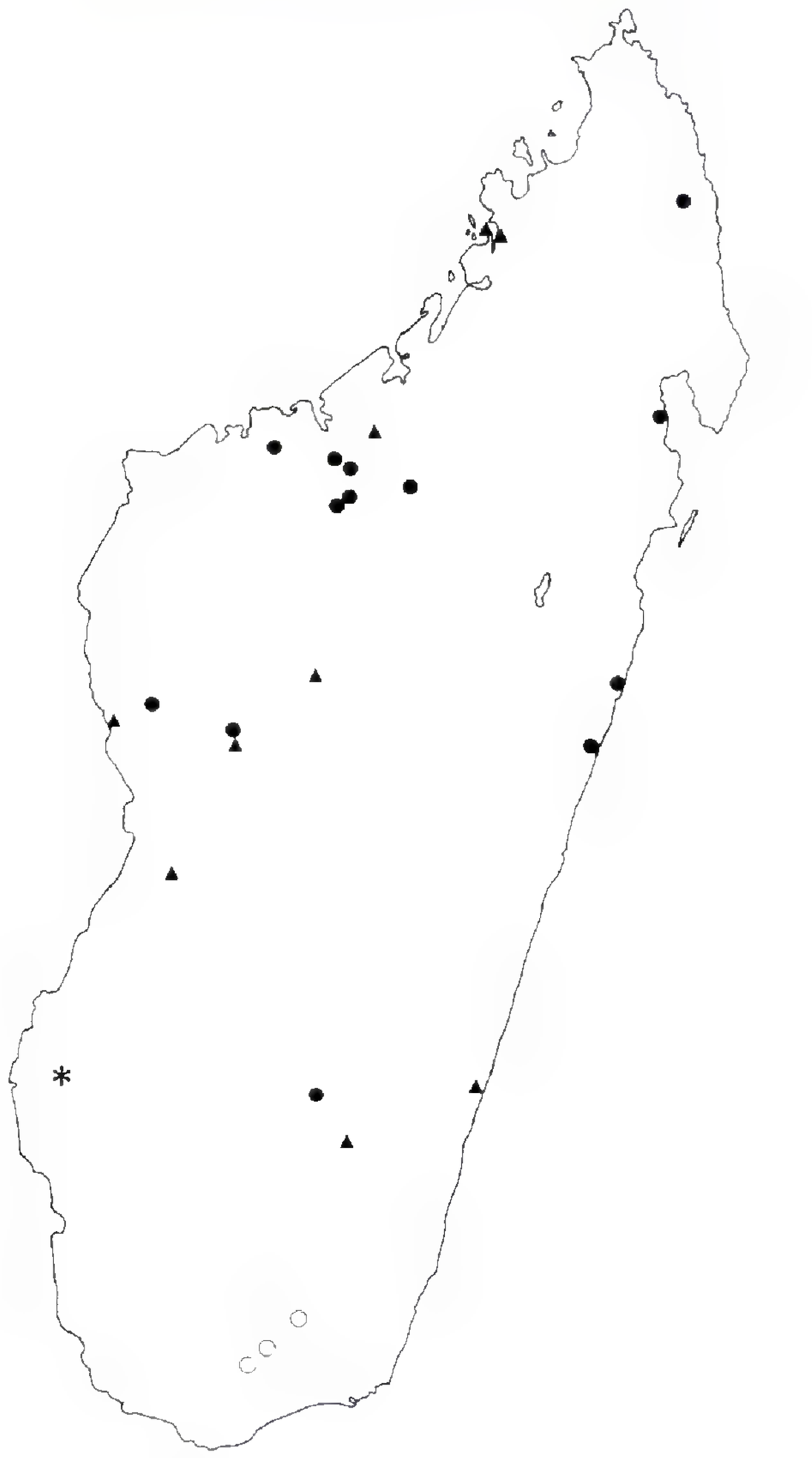
Although the rugose endotesta of the seed suggests an affinity with *Margaritaria indica,* the large staminate flowers set *M. cyanosperma* apart from all of the other species in the genus. Unfortunately, the species remains poorly known, and the typification of its name remains somewhat doubtful. It is impossible to tell from Gaertner's description, based on the fruit alone, which of the two species of *Margaritaria* on Sri Lanka should take the epithet *cyanosperma.* According to Dr. W. Frey, of Universität Tübingen (pers. comm.), the "type material" of Gaertner's is missing and presumed lost. However, since Thwaites (1856) clearly distinguished the two species, I am (in the absence of any contrary evidence) following his usage in assignment of names and am designating the specimen cited by him as neotype.

9. **Margaritaria rhomboidalis** (Baillon) Webster, comb. nov. *Cicca ? rhomboidalis* Baillon, Adansonia I. 2: 51. 1861. *Phyllanthus ? rhomboidalis* (Baillon) Mueller-Arg. Linnaea 32: 52. 1863, in DC. Prodr. 15(2): 417. 1866; Leandri, Not. Syst. Paris 6: 199. *fig. V.* 1938. Fl. Madagascar 111(1): 97. *fig. XV, 6–11.* 1958. TYPE: Madagascar, Ambongo, *Perville 664* (P, lectotype). FIGURE 3.

Shrub or small tree ca. 3–8 meters high; twigs pale, subterete; foliage deciduous. Leaf blades chartaceous to subcoriaceous, elliptic to obovate, ca. 2–5(–7) cm. long, 1.5–3 cm. broad, mostly obtuse to acute at tip, cuneate and often inequilateral at base, usually greenish on both sides (sometimes more or less glaucous beneath); veins (ca. 7 to 12 on a side) and veinlets conspicuous, prominulous especially beneath; margins plane or slightly reflexed; petioles 3–7(–13) mm. long, plane to adaxially channeled; stipules caducous, brownish, scarious, oblong-lanceolate, 1.2–4 mm. long. Staminate flowers several per axillary cluster; pedicels 3–5 mm. long; sepals 4, biseriate, ovate, entire, 1.8–2.5 mm. long, 1.3–1.7 mm. broad; disc obscure or absent; stamens 4, the filaments free, 0.5–1.2 mm. long, the anthers oblong, (0.8–)1–1.4 mm. long. Pistillate flowers solitary; pedicels compressed-angled, becoming 4–12(–20) mm. long; sepals 4, biseriate, ovate, entire, 2–3.2 mm. long; disc obscure or absent; ovary of 2 or 3 carpels, the styles usually basally connate, column 0.8–1.2 mm. high, the tips bifid and recurving, 0.5–1 mm. long. Capsules subglobose, irregularly dehiscent, mostly 8.5–10(–12) mm. in diameter, the endococci thin and papery, the columella more or less persistent, ca. 4–5 mm. long; seeds with thickish sarcotesta (whitish on drying), the endotesta more or less ribbed or rugose, 2.8–4.5 mm. long, the hilum varying in position from adaxial to abaxial, ca. 0.5–0.8 mm. across.

DISTRIBUTION. Endemic to Madagascar, mostly in deciduous forest or scrub at 300 meters or below (MAP 6).

SPECIMENS EXAMINED. **Madagascar.** FIANARANTSOA: bassin de la Menarahaka,



MAP 6. Distribution of *Margaritaria* in Madagascar. Solid dots, *M. anomala*; open circles, *M. decaryana*; triangles, *M. rhomboidalis*; asterisk, *M. hispidula*.

à l'est d'Ihosy aux environs d'Ambinda, *Capuron 11621, 11623* (P); Ankirihitra, près du mont Tsitondroina, *Perrier de la Bâthie 1346* (P); forêt de Belambo, nord de Marohala, *SF 16238* (P). MAJUNGA: forêt de Tsiampihy [Tsiempihy], *Leandri, Capuron, & Razafindrakoto 2195* (P); l'Antsingy, vers Ambodiriana, *Leandri, Capuron, & Razafindrakoto 2338* (P), *Leandri & Sabourеau 2720, 3069* (P). TULEAR: Tsingy du Bemaraha, *Leandri 948, 954* (P).

This species, which appears to be rather common and widespread in Madagascar, resembles *Margaritaria indica* in the rugose endotesta of the seed, but differs in the distinctly prominulous leaf venation, obscure staminate disc, larger anthers, and connate styles.

10. **Margaritaria anomala** (Baillon) Fosberg, Kew Bull. 33: 185. 1978.

Cicca anomala Baillon, Étude Gén. Euphorb. 619. 1858. *Phyllanthus anomalus* (Baillon) Mueller-Arg. Linnaea **32:** 52. 1863; in DC. Prodr. **15**(2): 418. 1866. TYPE: "Madagascar," *du Petit-Thouars s.n.* (P, holotype).

Flueggea major Baillon, Étude Gén. Euphorb. 593. 1858; Adansonia I. **2:** 42. 1861. *Phyllanthus hysteranthus* Mueller-Arg. Linnaea **32:** 52. 1863 (*nomen superfl.*). TYPE: Mauritius, *Bouton s.n.* (P, holotype).

Flueggea ? eglandulosa Baillon, Étude Gén. Euphorb. 593. 1858. *Phyllanthus erythroxyloides* Mueller-Arg. in DC. Prodr. **15**(2): 418. 1866; Leandri, Fl. Madagascar **111**(1): 94. *fig. XV, 1–5*. 1958. *Phyllanthus eglandulosus* (Baillon) Leandri, Catal. Pl. Madagascar, Euphorb. 23. 1935. *Phyllanthus anomalus* subsp. *erythroxyloides* (Mueller-Arg.) Leandri, Not. Syst. Paris **6:** 191. 1938. TYPE: Madagascar, Ambongo, *Perville 662* (P, holotype).

Phyllanthus cheloniphorbe Hutchinson, Kew Bull. **1918:** 204. 1918. *Margaritaria anomala* var. *cheloniphorbe* (Hutch.) Fosberg, Kew Bull. **33:** 185. 1978. TYPE: Aldabra, *Abbott s.n.* (K, lectotype; US, isotype).

Glabrous shrub or small tree 1–6 meters high; bark scaly or in strips; foliage partly or wholly deciduous; twigs brownish, smooth, subterete or compressed. Leaf blades thinly chartaceous, elliptic to obovate or spathulate, (2–)3–6(–10) cm. long, 1.5–4(–6) cm. broad, rounded or emarginate to obtuse or bluntly cuspidate at tip, cuneate at base (more or less decurrent on petiole), usually paler (sometimes glaucous) beneath; veins and veinlets obscure to prominent but veinlet reticulum usually not prominulous beneath; leaf margins more or less incurved to revolute; petiole 2–6 (–10) mm. long, plane or adaxially somewhat channeled; stipules caducous, brownish-scarious, oblong-lanceolate, acuminate or blunt and apiculate, 2.5–5 mm. long. Staminate flowers several per axillary cluster; pedicels mostly 3–5 mm. long; sepals 4, biseriate, usually the outer ones 1.2–2 mm. long, 1–1.3 mm. broad, ovate, entire, the inner ones larger, 1.5–2.3 mm. long, 1.3–2 mm. broad; disc adnate, smooth or rugulose, mostly 0.5–1 mm. across; stamens 4, the filaments free, becoming 1–1.5 mm. long, the anthers 0.8–1.4 mm. long. Pistillate flowers solitary or less often paired at proximal axils of annual increment of growth; pedicels more or less compressed and angled, 5–15(–20) mm. long; sepals 4, biseriate, ovate to oblong, entire, 1.5–2.5 mm. long; disc entire, adnate, 1–2.2 mm. across; ovary of 2 (very rarely 3) carpels, the styles free or basally coherent, ca. 0.8–1.5 mm. long, bifid, with the branches more or less sharply reflexed. Fruits subglobose or laterally compressed, indehiscent or irregularly dehiscent, 6–8 mm. in diameter, endococci not developed (wall layers not separating), columella not persistent; seed with thin, bluish sarcotesta, the endotesta smooth (rarely somewhat rugose), more or less planoconvex or trigonous-lenticular, (2.7–)3.5–5.5 mm. long, the hilum adaxial, circular, sub-basal, 0.9–1.2 mm. across.

DISTRIBUTION. Scrub or seasonal forests below 1000 meters; Madagascar, Aldabra, Astove, and Mauritius (MAPS 5, 6). Reported from Cosmoledo by Fosberg (1978).

SPECIMENS EXAMINED. **Aldabra Islands.** Without further locality, 1892, *Abbott s.n.* (US). ÎLE MICHEL: scrub on sandy champignon, *Fosberg 49357* (DAV). MIDDLE ISLAND: scrub, moderately rough limestone, *Fosberg 49582, 49666, 49671* (DAV). SOUTH ISLAND: scrub on flat limestone, *Fosberg 48848, 48961, 49029, 49309, 49401* (DAV). **Astove Island:** Grand Anse, scrub on moderately

rough limestone, *Fosberg 49715, 49736* (DAV). **Comoro Islands.** Without further locality, *Boivin s.n.* (K, P). GRANDE COMORE: Moroni, *d'Alleizette s.n.* (L). **Madagascar.** DIEGO SUAREZ: forêt entre Ambondsofe et Ambodimagoro, plateaux calcaires, 250 m., *Humbert 18993* (P). FIANARANTSOA: vallée d'Ihosy, 800–1000 m., rochers siliceux, *Humbert 2998, 2998ter* (P). MAJUNGA: Berizoka, *Perrier de la Bâthie 339* (P); collines seches, Maevatanana, *Perrier de la Bâthie 339bis* (P); vallée de Menavava, *Perrier de la Bâthie 339ter* (P); bois secs, Bemarivo, *Perrier de la Bâthie 9527* (P); vallée de la Betsiboka à Marovoay, 50 m., bois du terrains arenacés, *Humbert & Perrier de la Bâthie 2353* (P); Ambongo, *Perrillé 662* (P); Ankarafantsika, Tsaramandroso, *Ramamoujisoa 2029* (P); Ankaraobato, Distr. Mitsinjo, *SF 5386* (P); station forestière de Marohogo, Majunga, *SF 7967* (P); forêt de Morarano, Marohogo, *SF 8069* (P); forêt Tsimembo,, Antsalova, *SF 8248* (P). TAMATAVE: côte littoral est, Baie d'Antongil, *d'Alleizette s.n.* (L); Andevoranto, Ambila-Lemaitso, *Ramasokoto 1524* (P); Tampina, forêt littorale, *Perrier de la Bâthie 13318* (P). TULEAR: Mandena-Ft. Dauphin, *SF 6609* (P). **Mauritius:** without further locality, *Ayers s.n.* (K), *Blackburn s.n.* (K), *Boivin s.n.* (P), *Bouton s.n.* (A, K), *Commerson s.n.* (P), *Duljeet MAU 11640, MAU 16638* (MAU), *Grey s.n.* (K); lisière des bois au Pouce et dans l'Anse Courtois, *Boivin s.n.* (P); Mt. Corps de Grade, *Friedmann 2620* (P); *Coode et al. 5021, 5022* (K); Montagne Ory, *Friedmann & Lorence 2626bis* (P); Petite Rivière, dry forest, *Herb. Royal Gardens Pamplemousse 139* (K); Plaine des Roches, *Julien MAU 14164* (MAU); Ferme Cascade, *Vaughan MAU 1611* (MAU).

Hooker (1887) treated *Margaritaria anomala* as a synonym of *M. indica*, apparently on the basis of some Wallich specimens misidentified by Mueller (1866). However, although staminate specimens are difficult to distinguish, the indehiscent, 2-carpellate fruits of *M. anomala* are very different from the dehiscent, 3-carpellate ones of *M. indica*.

Leandri (1958) has attempted to separate *Phyllanthus anomalus* from *P. erythroxyloides* on the basis of fruit and leaf shape. However, as noted by Coode (1978), the type specimen of Petit-Thouars was probably collected on Mauritius rather than on Madagascar. There is unfortunately some uncertainty in applying the name *Phyllanthus erythroxyloides*, since Baillon's allusion to the obsolete floral disc in his brief description (of *Flueggea eglandulosa*) would suggest that he might have had material of *Margaritaria rhomboidalis*. However, the leaves of the type collection (*Perrillé 662*) lack the prominulous venation characteristic of *M. rhomboidalis*, and the pistillate flower does have a disc. At any rate, the Mauritius and Madagascar populations clearly seem to be conspecific, and the name *M. anomala* applicable to both.

Fosberg (1978) has separated the populations from Aldabra and adjacent islands as var. *cheloniphorbe*. However, he does not cite any diagnostic characters, and although the Aldabra specimens do tend to have thicker and more rounded leaves, I can find no significant and consistent differences in leaves, flowers, or fruits between the plants of Aldabra and those of Mauritius and Madagascar.

11. **Margaritaria dubium-traceyi** Airy Shaw & Hyland, Kew Bull. 31: 357. *fig. 1.* 1976. TYPE: Queensland, *Hyland 7937* (K, holotype, *n.v.*).

Glabrous shrub or tree to 5 meters high; twigs terete, grayish, with scattered lenticels. Leaf blades chartaceous to subcoriaceous, ovate to elliptic-oblong, 4–6(–9) cm. long, 2–3.5(–5.5) cm. broad, emarginate, rounded or obtuse (rarely minutely apiculate) at tip, cuneate at base (distinctly decurrent on petiole), olivaceous; veins (ca. 6 to 9 on a side) and veinlets prominulous on both sides in a prominent reticulum; margins plane; petiole distinctly laterally carinate or adaxially channeled; stipules caducous. Staminate flowers several per axillary cluster; pedicels capillary, 10–13 mm. long; sepals 4, biseriate, elliptic to obovate, subequal, the outer ones ca. 1.2–1.3 mm. long, 0.8 mm. broad, the inner ones 1.5–1.8 mm. long, 0.8–1 mm. broad; disc angular, ca. 1 mm. across; stamens 4, the filaments united in pairs at base, 1.5–2.5 mm. long, the anthers elliptic, 0.3–0.5 mm. long. Pistillate flowers (not seen, descr. ex Airy Shaw) 1 or 2 per axil; pedicels slender, subterete or angled, 4–8 mm. long; sepals 4, biseriate, ca. 1 mm. long; ovary of 2 carpels, the styles basally connate, ca. 1 mm. long, bifid, branches spreading. Fruits subglobose or elliptic, more or less indehiscent (tardily splitting from apex), 5–7 mm. in diameter, endococci corneous (not tenuous and hyaline); seeds with bluish sarcotesta very tenuous except at base, the endotesta more or less ridged or grooved on back, wedge shaped, ca. 3.1–3.7 mm. long and 2.1–2.9 mm. across the back, the hilum basal, 0.2–0.3 mm. across.

DISTRIBUTION. Seasonal deciduous or eucalypt forests, below 600 meters; northern Queensland.

SPECIMENS EXAMINED. **Australia. Queensland.** BURKE DISTR.: Haydon Creek, Croydon–Normanton Road, alt. 60 m., *Hyland 5121* (DAV). COOK DISTR.: Springmount Road, 17°10′S, 145°15′E, alt. 550 m., *Hyland 5594* (K); betw. Chillagoe and Mungana, alt. 390 m., *Hyland 5838* (DAV); S. Palmer River cachement, 16°15′S, 144°40′E, alt. 480 m., *Hyland 5895* (DAV). Additional Queensland localities, cited by Airy Shaw (1976), have been indicated on MAP 5.

The relationships of *Margaritaria dubium-traceyi* are uncertain. The rugose endotesta of the seed suggests a possible affinity to *M. indica*, although the fruit is quite different and more similar to that of *M. anomala*. Possibly *M. dubium-traceyi* is a specialized derivative of *M. indica*, comparable to the vegetatively somewhat similar *M. luzoniensis*, and the resemblances in fruits with *M. anomala* are due to convergence.

12. **Margaritaria hispidula** Webster, sp. nov. FIGURES 2, 8.

Ab aliis speciebus Madagascariensibus differt foliis venis prominulis, infra hispidulis, capsulis mox dehiscentibus.

Tree 8 meters high; twigs subterete, whitish-hispidulous at tips, glabrate below, not prominently lenticellate. Leaf blades subcoriaceous,

shiny and subglabrous above, copiously hispidulous-hirsutulous beneath, ovate or elliptic to obovate, obtuse or subacute at tip, cuneate to rounded at base, ca. 2.5–4.5 cm. long, 1–2.5 cm. broad; major veins (6 to 8 on a side) and veinlet reticulum distinctly prominulous on both sides; margins plane or recurved; petioles 3–6 mm. long, copiously hispidulous-hirsutulous, not adaxially channeled; stipules oblong-lanceolate, scarious, pale brownish, 2.5–3.5 mm. long. Flowers not seen. Fruiting pedicels subterete, 9–11 mm. long, hispidulous; carpels 3, the styles (on immature fruit) ca. 2 mm. long, united about halfway into a column; fruits subglobose, 6–7 mm. in diameter, hispidulous, tardily dehiscent, the endocarp tough, 0.2 mm. thick, not fragile and papery; mature seeds not seen.

DISTRIBUTION. Known only from the type collection (MAP 6).

SPECIMEN EXAMINED. **Madagascar.** TULEAR: Befandrianda-Sud, neben Regenteich, 150 m. alt., *P. Otto Appert 107* (K, holotype).

It is regrettable that this species has to be proposed as new on the basis of such imperfect material. Vegetatively, it is similar to *Margaritaria rhomboidalis*, but its very different fruits suggest a closer relationship to *M. anomala* or *M. dubium-traceyi*. Although we cannot be certain of its affinities until better material is collected, I feel sure that the Appert collection represents a species distinct from the known Madagascan taxa.

13. **Margaritaria decaryana** (Leandri) Webster, comb. nov. *Phyllanthus decaryanus* Leandri, Not. Syst. Paris 6: 198. 1938; Fl. Madagascar 111(1): 98. *fig. 18, 1–5*. 1958. TYPE: Madagascar, Imangory, *Decary 8937* (P).

Phyllanthus decaryanus var. *manambia* Leandri, Mém. Inst. Sci. Madagascar **8B**: 228. *fig. 6, 1–5*. 1957. TYPE: Madagascar, between Tsivory and Imanombo, *Capuron 8543* (P, lectotype).

Glabrous shrub or small tree; twigs subterete, smooth, grayish or brownish; foliage deciduous. Leaf blades membranous, broadly elliptic or suborbicular to spathulate or obcordate, 1.0–1.8 cm. long, rounded to emarginate at tip, cuneate at base, green on both sides (somewhat paler beneath); major veins mostly 3 or 4 on each side, veinlet reticulum somewhat prominulous beneath; margins plane; petioles ca. 3–5 mm. long, adaxially channeled; stipules persistent or caducous, oblong, scarious, acute and more or less denticulate-fimbriate distally, 1.0–2.5 mm. long. Staminate flowers several per cluster; pedicels slender, 4–6 mm. long; sepals subequal, becoming reflexed, elliptic or ovate, obtuse, entire or obscurely denticulate at apex, 1.6–2.1 mm. long, 1.1–1.8 mm. broad, disc entire, thin, ca. 0.7–1 mm. across; stamens 4, the filaments connate below, mostly 1.5–2.2 mm. long (staminal column 0.8–1.5 mm. long), the anthers oblong, 0.8–1.1 mm. long. Pistillate flowers solitary or paired; pedicels angled-compressed, ca. 3–4 mm. long; sepals 4, subequal, 2–2.5 mm. long, 1.5–2.5 mm. broad; disc thin, entire, ca. 1.5 mm. across; ovary

of 2 or 3 carpels, the styles more or less erect, 1.5–2 mm. long, basally connate, distally bifid. Fruits not seen.

DISTRIBUTION. Xeric scrub; southern Madagascar (MAP 6).

SPECIMENS EXAMINED. **Madagascar.** TULEAR: restes de bush, entre Tsivory et Imanombo, *Capuron 8543, 8543bis* (P); environs d'Ampandrandava, entre Bekily et Tsivory, *Seyrig 242B* (P).

If I am correct in associating Leandri's var. *manambia* with his *Phyllanthus decaryanus*, then the species is well characterized by its monadelphous androecium and small suborbicular leaves. Leandri refers to the species and variety as each having 2-locular ovaries, but actually they appear to be 2-locular in *Capuron 8543bis* and 3-locular in *Seyrig 242B*.

14. **Margaritaria obovata** (Baillon) Webster, comb. nov. *Flueggea obovata* Baillon, Adansonia I. 2: 41. 1861 (non *Securinega obovata* Mueller-Arg. 1866). *Securinega bailloniana* Mueller-Arg. in DC. Prodr. 15(2): 451. 1866. *Flueggea bailloniana* (Mueller-Arg.) Pax, Bot. Jahrb. 19: 76. 1894. TYPE: Zanzibar, *Boivin s.n.* (P, holotype). FIGURES 9, 10.

Margaritaria discoidea var. *triplosphaera* Radcliffe-Smith, Kew Bull. 30: 680. 1976. TYPE: Tanzania, Songea, *Milne-Redhead & Taylor 8373* (K, holotype, *n.v.*).

Shrub or tree 2–10 meters high; branches subterete, reddish- or brownish-hirtellous at growing tips, glabrate and grayish in age; foliage usually deciduous. Leaves chartaceous; blades mostly obovate or spathulate, (1–)2–4(–5) cm. long, 1–3 cm. broad, usually rounded or very obtuse at tip, cuneate at base, above smooth, beneath more or less glaucous and hirtellous especially along midrib; major veins mostly 7 to 12 on a side, raised beneath, veinlet reticulum more or less prominulous; margins recurved or narrowly revolute; petioles usually hirsutulous, not adaxially channeled, 2–4(–5.5) mm. long; stipules caducous, lanceolate, acuminate, ca. 2–3.5 mm. long. Staminate flowers several per axil; pedicels glabrous, 3–5 mm. long; sepals biseriate, the outer ones oblong, 1.5–2 mm. long, 0.7–1 mm. broad, the inner ones broadly obovate, (1.5–)2–2.5 mm. long, 1.2–1.6 mm. broad; disc 0.5–1 mm. across; stamens 4, the filaments becoming 1.3–1.8 mm. long, the anthers linear-oblong, (0.6–)0.8–1 mm. long. Pistillate flowers solitary or paired; pedicels often hirsutulous, mostly 2.5–6 mm. long in fruit; sepals 4, subequal, oblong, hirsutulous on back, 1.6–2.5 mm. long, 1.3–2 mm. broad; disc thin, 1.7–2.0 mm. across; ovary deeply trilobed, hirsutulous; carpels 2 (22 percent) or 3 (78 percent), very rarely 4, the styles free or nearly so, spreading, bifid to bipartite, 1.2–1.5 mm. long. Capsules deeply 2- or 3-lobed (most often only 2 carpels well developed), mostly 10–12 mm. in diameter, the cocci subspheroidal, usually hirsutulous, the endocarp hyaline-papery; endotesta of seed plano-convex, smooth or grooved on back, 3.8–4.5 mm. long.

DISTRIBUTION. Scrubland, deciduous forest, or savanna woodland, sea level to ca. 1000 meters; Burundi and Kenya south to Mozambique. Radcliffe-Smith (1976) cites a large number of additional localities, including records from Zaire and Zambia (MAP 4).

SPECIMENS EXAMINED. **Burundi.** BUBANZA: colline Muzinda, 900 m., *Lewalle 1240* (MO); Randa, savane boisée, 900 m., *Lewalle 2635* (NY). BURURI: Mutambara, forêt claire, 1000 m., *Reekmans 1077* (MO); Rumone, forêt claire sur rochers, 900 m., *Lewalle 1604* (MO). **Kenya.** COAST: Kilifi, Sokoke, *Gisau SOK6* (PRE), *SOK11* (K, PRE). **Malawi.** NORTHERN: Karong Distr., 2 mi. N. of Chilumba in Vinthukhutu Forest Reserve, *Brachystegia* woodland, 1800 ft., *Pawek 12064* (DAV). **Tanzania.** COAST: Pande Hill, 80 km. WNW. of Dar-es-Salaam, 250 ft., wooded grassland, *Harris, Tadros, & Mwasumbi BJH 3616* (MO); Umbungo, scrubland, 50 m., *Mwasumbi LBM 10477* (MO); Kisarawe Distr., *Semsei 3682* (PRE); 21 mi. S. of Dar-es-Salaam on Kilwa Rd., 150 m., *Harris & Rodgers BJH 3970* (MO). MOROGORO: Kilosa, *Semsei 3332* (PRE). NORTHERN: probably from Ukerewe Is., *Father Conrads 6035* (PRE). SOUTHERN HIGHLANDS: Kyimbila Distr., *Stolz 1744 (ex p.)* (A, MO, P), *1771* (A, GH, MO, NY, P, PRE). TANGA: Korogwe Distr., Kwamarukanga, *Shabani 57* (PRE); Mkono, 30 km. E. of Handeni, 518 m., *Archbold 1728* (MO). ZANZIBAR: *Sacleux* (P); Kidichi, 300 ft., *Faulkner 2751* (NY).

This distinctive species, which is widespread in east Africa, is sympatric with *Margaritaria discoidea* over essentially all of its range and has often been confounded with it, although Pax clearly distinguished the two in 1895 (under the names *Flueggea bailloniana* and *F. nitida*). Radcliffe-Smith (1976) provides thorough documentation of its distribution and discusses its relationship with *M. discoidea*, but conservatively treats it as a variety. However, *M. obovata* is clearly distinguished by the deeply lobed fruit (FIGURE 9), the usually distinctive pubescence (on fruits as well as leaves), and leaves with blades that are not decurrent on the petiole as adaxial flanges (a very useful character pointed out by Radcliffe-Smith). In this genus where distinguishing characters are difficult to find, *M. obovata* is much more clearly marked than most taxa, and I believe that it deserves full specific status.

DOUBTFUL AND EXCLUDED TAXA

Margaritaria oppositifolia L. in Alm, Pl. Surinam. 16. 1775, *nomen illegit.* = Combretaceae (Mueller-Arg. in DC. Prodr. **15**(2): 414. 1866).

Phyllanthus ankarana Leandri, Bull. Soc. Bot. France **81**: 452. 1934. TYPE: Madagascar, Ankara, *Perrier de la Bâthie 1174* (P, *n.v.*). Although Leandri referred this species to *Phyllanthus* section *Prosorus*, the staminate disc of separate segments is not correct for *Margaritaria*. In the later treatment by Leandri (Fl. Madagascar **111**(1): 102. *fig. XVI, 4, 5.* 1958), it is clear that the plant is a true *Phyllanthus*, neither of sect. *Cicca* nor of *Margaritaria*.

Phyllanthus flacourtioides Hutch. Kew Bull. **1915**: 48. 1915. SYNTYPES: Mozambique, Lourenço Marques, *Schlechter 11598, 11634* (K, *n.v.*). Hutchinson related his species to *Margaritaria discoidea*, and his description suggests that it may be a form of *M. discoidea* subsp. *nitida*. However, if

Hutchinson's description of the staminate specimen is correct, it cannot be a *Margaritaria*.

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Standley, P. C., *11711*, *12280*, *22250*, *23320*, *23509*, *24594*, *25988*, *26725*, *30813*, *30975*, *41045* (1).
Staudt, A., *927* (2a).
Stehlé, H., *979* (1).
Steinbach, J., *3481*, *6510*, *6541*, *6542*, *7251*, *7374* (1).
Stern, W. L., K. L. Chambers, J. D. Dwyer, & J. E. Ebinger *768*, *919* (1).
Sterringa, J. T., *12441*, *12529* (1).
Stewart, E. C., *14* (1).
Steyermark, J., *45807*, *47781*, *48053*, *51076*, *51413*, *51416*, *51493*, *62825*, *87008*, *89075*, *89078*, *89234*, *107569* (1).
Steyermark, J., G. Bunting, & C. Blanco *102101*, *102279* (1).
Stolz, A., *1744* (2b, 14); *1770* (2b). *1771* (14).
Stork, H. E., *19* (1).
Strey & Moll *3751* (2b).
Sulit, M. D., *3936* (7).
Talbot *1173* (7).
Tanner, R. E. S., *2788*, *3774*, *5349* (14).
Tejera, E., *36*, *182* (1).
Tessmann, G., *3064*, *3939*, *3978* (1).
Teunissen, M., *LBB 15060* (1).
Thiebaud, A., *838* (2b).
Thollon *39* (2a).
Thomas, N. W., *6081*, *10525* (2a).
Thwaites, G. H. K., *CP 2155*, *CP 2601* (8); *CP 3099* (7).
Tinley, K. L., *184*, *406* (2b).
Tisserant, R. P., *501*, *586*, *797*, *990*, *1783* (2a).
Tonduz, A. O., *13924* (1).
Troupin, G., *12520*, *12595* (2a).
Tsang, W. T., *29583*, *30219* (7).
Tuley, P., *1502* (2a).
Ule, E., *9573* (1).
Vaughan, R. E., *MAU 1611*, *MAU 3372*, *MAU 12172* (10).
Versteegh, C., & R. W. den Outer *29*, *228*, *311*, *480* (2a).
Vidal, S., *1729* (7).
Vigo, J. S., *6833*, *8043* (1).
Volkens, G., *1737* (2b).
Vuillet *247* (2a).
Wass, S., *663* (7).
Wagner, R. J., *1021*, *1927* (1).
Ward, C. J., *2474*, *2677*, *2819*, *3367*, *6038*, *6058*, *6715* (2b).
Warming, E., *1542* (1).
Weber, C. M., *1195* (7).
Webster, G. L., *4150* (1).

Webster, G. L., W. P. Adams, K. Miller, & L. Miller *12000* (1).
Webster, G. L., J. Ellis, & K. I. Miller *9157* (1).
Webster, G. L., E. Samuel, & T. Williams *10514* (3).
Welwitsch, F., *340* (2a).
Wedermann, E., *2549* (1).
Wgoni, J. F., *65* (2b).
White, C. E., *993* (1).
White, F., *3490*, *3600*, *6326* (2b).
Wight, H., *2599* (7).
Wild, H., *4160* (2b).
Wilde, J. E., & J. T. Baldwin, Jr. *41* (1).
Wilde, W. J. J. O. de, & B. E. E. de Wilde-Duyfyes *2374* (2a).
Williams, L., *565*, *2481*, *3404*, *4930*, *8806*, *10255*, *10272*, *11845*, *13304* (1).
Williams, L. O., *15954* (1).
Williams, L. O., & A. Molina *10137*, *10293*, *12703*, *14107* (1).
Williams, R. O., *12014* (1).
Wilson, P., *8394* (3).
Winit *1957* (7).
Winter, B. de, & J. Vahrmeijer *8601* (2b).
Winzerling, H. W., *11-19* (1).
Wright, C., *584a*, *1931*, *1932*, *1933* (1); *1436* (3); *1437* (3, 4); *583*, *584* (4).
Wurdack, J. J., & J. V. Monachino *39689*, *41411* (1).
Yuncker, T. G., J. M. Koeppen, & K. A. Wagner *8154* (1).
Zenker, G., *927*, *2053*, *2083*, *2530*, *2890*, *3138*, *4203* (2a).

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A BIOSYSTEMATIC REVISION OF BOMMERIA

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BOMMERIA IS A GENUS of ferns found in xeric and seasonally dry mountainous regions of the southwestern United States, Mexico, and Central America. The genus was first described by Fournier (1876), who named it for the Belgian pteridologist Jean Edouard Bommer. Prior to the present study, the most complete work discussing species relationships in *Bommeria* was that of Maxon (1913), who delimited the genus based on its characteristic pedate lamina and strigose indument and differentiated its four species primarily on variation in venation and leaf size. In 1942, based on the Chihuahuan collections of Irving Knobloch, Maxon added another species to the genus but did not otherwise alter his concept of species boundaries. A more complete historical treatment of the taxonomy and generic affinities of *Bommeria* has recently been presented elsewhere (Gastony & Haufler, 1976).

The distribution of spores along the veins in *Bommeria* species commonly allies the genus with the "gymnogrammoid" ferns (e.g., *Hemionitis* L. and *Gymnopteris* Bernh.). Some morphological features of *Bommeria* species, including leaf margin sporangial distribution and reticulate spores (see Haufler & Gastony, 1978b), however, are usually associated with the "cheilanthoid" genera (e.g., *Doryopteris* J. Sm. and *Cheilanthes* Sw.). These two suprageneric groups are not adequately separated from each other, and intergeneric distinctions within the groups are imprecise. Since *Bommeria* shares gymnogrammoid and cheilanthoid features, understanding species relationships in this genus may be valuable in recognizing evolutionary lines and in defining the natural limits of related genera.

Live material of all previously recognized species of *Bommeria* was collected in the field. Sporophytes of these collections were subsequently cultured under greenhouse conditions, and their gametophytes were grown on agar in the laboratory. A series of reports based on work with these living plants and herbarium specimens has discussed chromosome counts and apomixis (Gastony & Haufler, 1976), antheridiogen and breeding systems (Haufler & Gastony, 1978a), fine structure and ontogeny of spore walls (Haufler & Gastony, 1978b), and flavonoid constituents (Haufler & Giannasi, in prep.) in this genus. These papers have provided information relevant to understanding species relationships and evolution in *Bommeria* and have addressed some general aspects of apogamy, outcrossing, and spore wall structure in the ferns. The present paper focuses on description of gametophytic and sporophytic organs and examines taxonomically critical aspects of hybridization and foliar ontogeny. In addition, it synthesizes the data accumulated from the entire series of studies into a realistic taxonomic revision of the genus and clarifies the relationship of certain other genera to *Bommeria*.

MATERIALS AND METHODS

Materials for anatomical study were fixed in either Craf IV or FPA (Berlyn & Miksche, 1976), dehydrated in an alcohol series, mounted in paraffin, and sectioned on a rotary microtome at 12 μm. thickness. The sections were affixed to slides using Haupt's adhesive (Berlyn & Miksche, 1976) and stained with either a modified safranin–fast green series or haematoxylon.

Critical point drying was used to prepare leaves for scanning electron microscope examination of surface features. Leaf portions were fixed in FPA, dehydrated in an alcohol series, transferred to amyl acetate, and critical point dried. After having been undercoated with carbon and coated with gold-palladium, the leaf surfaces were examined and photographed with an ETEC instrument at 20 KV.

Leaf clearings were prepared following a technique modified from Dilcher (1974). Leaves were heated in 10 percent NaOH until translucent. To effect complete clearing, the leaves were placed in 50 percent to full strength commercial bleach and subsequently in a saturated chloral hydrate solution. Following a dehydration series to 95 percent ethyl alcohol (EtOH), the leaves were stained in a 1 percent solution of safranin in 95 percent EtOH for two days. Leaves were then dehydrated, placed in xylene, and mounted between thin glass plates in synthetic resin (Permount).

Methods of analysis for study of gametophyte ontogeny and morphology, including preparation of spores, growth medium compositions, and cultural conditions, are as discussed in Haufler and Gastony (1978a).

Although crossing experiments are important in angiosperm biosystematics, crossability is rarely investigated in ferns. The bisexual, free-living gametophyte complicates controlled crosses in homosporous pteridophytes. Lovis (1968) developed the "Leeds" method of fern hybridization, which uses unisexual gametophytes to eliminate the possibility of self-fertilization and to reduce the variables inherent in working with fern gametophytes. This method has been modified and adapted here for use with *Bommeria* species, the breeding system of which facilitates the culture of unisexual gametophytes (Haufler & Gastony, 1978a). Male gametophytes from one parental population were placed in a small pool of water on a depression slide to test for active sperm release. Female gametophytes from the second parental population were introduced into the pool and observed for the opening of archegonial necks. After most sperm activity had ceased, the archegonial gametophytes were removed from the water and assayed for sporophyte production.

RESULTS

MORPHOLOGY AND ANATOMY OF SPOROPHYTE ORGANS

RHIZOME. The rhizome has two distinct forms. In *Bommeria hispida* it is slender (3 mm. or less in diameter) and has a creeping growth habit

with the nodes at 7–10 mm. intervals. In the other *Bommeria* species, the cortex forms a thick layer, and the overlapping petioles, spaced at ca. 1 mm. intervals, contribute to a more robust rhizome.

The stele in all species is a solenostele (FIGURES 1, 2), but, where internode lengths are reduced, a dictyostelic condition prevails. The cortex and pith of the rhizome are composed of tightly packed and often deeply pigmented cells (FIGURE 1). Most often, a majority of the cortical cells appear to be dead. These cells probably function to protect the rhizome from mechanical damage, animal invasion, and dessication.

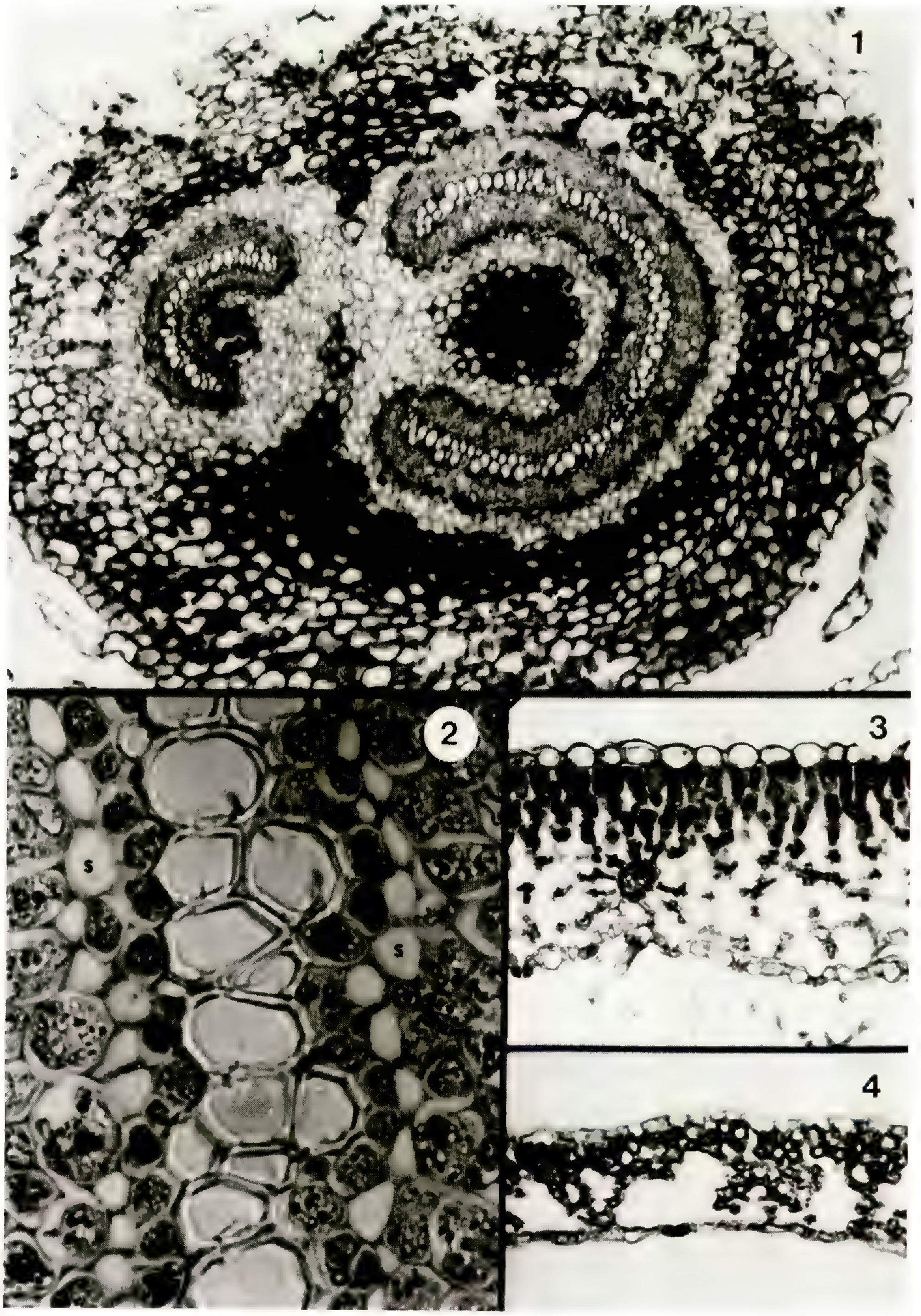
Rhizome indument consists of scales and trichomes that are apparently originally associated with growing points. As the rhizome matures, these indument features are replaced in function by the thick, impermeable cortex and are often largely or entirely lost. In *Bommeria hispida*, perhaps because of greater elongation of the rhizome, there are relatively fewer scales and trichomes than are present on mature rhizomes of other species.

Leaves are arranged in a distichous fashion along the rhizome. Branching is more prevalent in the creeping rhizome of *Bommeria hispida* than in the short rhizomes of the other species. Dichotomous rhizome branching characterizes the genus and can lead to a matlike growth in *B. hispida*. Vegetative reproduction can result from branching and subsequent degeneration of the older plant portions.

LEAF. **Petiole.** Petiole characters are influenced by environment and plant maturity; as a result they are quite variable. Under standardized greenhouse conditions, for example, the petiole of a developing leaf of *Bommeria hispida* that is fully exposed to the sun may elongate only 4–5 cm. during development. On the same plant, however, if the petiole of a developing leaf is crowded by decaying leaves or shaded by mature leaves, it may become 10–12 cm. long. Petiole thickness also varies with plant maturity and growing conditions. Fertile leaves of *B. ehrenbergiana* have petioles that range from 1 mm. to greater than 3 mm. in diameter.

There is a single vascular trace in the petiole from initiation in the rhizome to the base of the blade, at which point the trace divides into the three major veins of the pedate blade. The degree of sulcation of the petiole seems directly related to its diameter: the petioles of small diameter, as in *Bommeria hispida*, seldom have sulci, while the more robust petioles of *B. ehrenbergiana* almost always have a sulcus in their adaxial surfaces. Although petiole color is quite variable, there is a gradation from the general condition of castaneous petioles in *B. hispida*, to darker-hued petioles in *B. subpaleacea* and *B. pedata*, and finally to the usually atro-purpureous petioles of *B. ehrenbergiana*. This trend can be seen when leaves of different species grown under uniform conditions are compared; however, immature leaves or those grown under conditions of low light intensity have lighter petiole colors.

Indument in general, and especially that associated with the petiole, is deciduous. In addition, there is a general tendency for that of older herbarium specimens to be less dense. To assess petiole indument features,



FIGURES 1–4. Anatomy of **Bommeria** plant organs. 1–3, *B. hispida*: 1, rhizome stele, cross section, × 75, showing amphiphloic siphonostele and leaf trace; 2, enlargement of rhizome stele, × 500, showing arrangement of cell types; 3, cross section of leaf, × 100. 4, *B. ehrenbergiana*, cross section of leaf, × 100. Abbreviations: LT = leaf trace; p = phloem; pe = pericycle; pp = phloem parenchyma; s = sieve cell; x = xylem.

data from herbarium specimens can be augmented by comparative evidence from greenhouse grown plants. These combined observations show that leaves of all species have petioles with scales and trichomes early in leaf ontogeny. As the leaf matures, however, much or all of this indument dries up and falls off. The distribution of scales and trichomes is influenced by environmental conditions: dry conditions promote a dense investiture of scales and trichomes, while moist conditions elicit a more sparse development. Plants grown under standardized greenhouse conditions show the petioles of *Bommeria hispida* to have the most abundant trichomes and scales, those of *B. subpaleacea* to have slightly fewer, and those of *B. ehrenbergiana* and *B. pedata* to be almost glabrous. In all species, the petiole base bears numerous scales that are perhaps a remnant of the bud-protecting scales.

Lamina. The lamina of fern leaves accounts for most of the interspecific variation and so provides the bulk of morphological characters used in assessing relationships.

Anatomy. The leaf anatomy of *Bommeria hispida* distinguishes it from the other species. The thickness of the palisade layer in leaves of *B. hispida* (FIGURE 3) is 2 or 3 cells, while in other species it is lacking or 1 or 2 cells (FIGURE 4). The remaining leaf mesophyll tissue is more densely arranged in *B. hispida* than in other *Bommeria* species.

Stomates. The stomates of all *Bommeria* species are anomocytic, as are those of most genera that have been examined in the Pteridaceae (Van Cotthem, 1970).

Although stomatal arrangements are not taxonomically significant in *Bommeria*, characteristics of the individual stomates are of interest. Unlike many plants adapted to xeric conditions, which often have leaves with thick cuticles and stomates that are sunken below the epidermal surface, *Bommeria* has stomates that are not sunken and that lack noticeably thickened cuticular deposits. The stomates, in fact, protrude slightly above the epidermis. Indument characters (discussed below) are perhaps influential in the control of water loss in *Bommeria* and so relieve the selection pressure for the evolution of other xeric adaptations.

Polyploid taxa often have larger guard cells than do their diploid congeners (see, for example, Tryon, 1968). Thus, in *Bommeria* it might be expected that guard cells of the triploid *B. pedata* would be larger than those of its diploid congeners. Measurements of guard cell length, however, fail to show a difference in size among *Bommeria* species. Guard cells in *B. pedata* range from 48 to 53 μm., well within the 36 to 58 μm. range of the other *Bommeria* species.

Venation. Maxon (1913, 1942) employed leaf venation as a principal character in distinguishing species of *Bommeria*. Indeed, it is the only well-defined character that he used to differentiate the erstwhile species *B. knoblochii* from *B. subpaleacea* (Maxon, 1942). He cited three types of venation in describing *Bommeria* species: free (or open) venation, in which veins branch dichotomously in traversing the lamina from the mid-

vein to the leaf margin but never anastomose; wholly areolate venation, in which all but the last (most marginal) vein branchings anastomose; and partially areolate venation, in which areoles only form adjacent to the three primary veins of the pedate leaf. Maxon, considering the venation of *B. subpaleacea* to be wholly areolate and that of *B. knoblochii* to be partially areolate, used this variation in distinguishing the two species.

Study of venation shows that a distinction between open and areolate venation is a reliable character, but that species delimitation based on wholly areolate versus partially areolate venation breaks down. Examination of specimens spanning the geographical range of each species shows that *Bommeria hispida* (FIGURE 6) and *B. pedata* (FIGURE 5) are never areolate, while *B. ehrenbergiana* (FIGURE 7) and *B. subpaleacea* (FIGURES 9, 10) always have some areolations. Among collections of *B. subpaleacea*, there is variation in the degree of areolate venation, but this variation is as likely to occur in a single population as between populations.

Leaf development emphasizes the distinction between the two patterns of venation. In leaves of species having free venation (FIGURES 11, 12), there are never any areoles present, even after the attainment of the pedate leaf form (FIGURE 12). Areoles are present, however, even in the small, reniform leaves that appear early in the heteroblastic series characteristic of species having areolate venation (FIGURES 13, 14). Therefore, no distinction between species can be made based on variation in the abundance or position of areoles.

Hickey (1973) has proposed and discussed a precise set of terms to be used in describing types of leaf venation. In an effort to standardize venation description, the terminology suggested by Hickey will be applied to *Bommeria*. All species of *Bommeria* have an actinodromous venation pattern. The three primary veins branch from a single point, are moderate in size, and follow a straight course. The secondary veins are identical in all species, having a moderate angle of divergence, being moderately thick, and following a straight course. Interspecific variation is seen in the tertiary and higher order veins. In the free-veined species, tertiary branching from the secondary veins results in discrete vein groupings (FIGURES 5, 6). The tertiary veins branch dichotomously, have a ramified branching pattern, and never rejoin the secondary veins. In net-veined species the tertiary vein groupings are not discrete; rather, they are interconnected by anastomoses. The branching pattern in these species is reticulate, and the tertiary veins closest to the secondary veins loop back and rejoin the secondaries (FIGURES 7, 9, 10).

Vernation. There has been some debate about the ubiquity of circinate vernation among the ferns. In *Botrychium*, for example, only the final leaf divisions exhibit circinate vernation, so this genus has been generally accepted as noncircinate (Clausen, 1938). Recently, however, Stevenson

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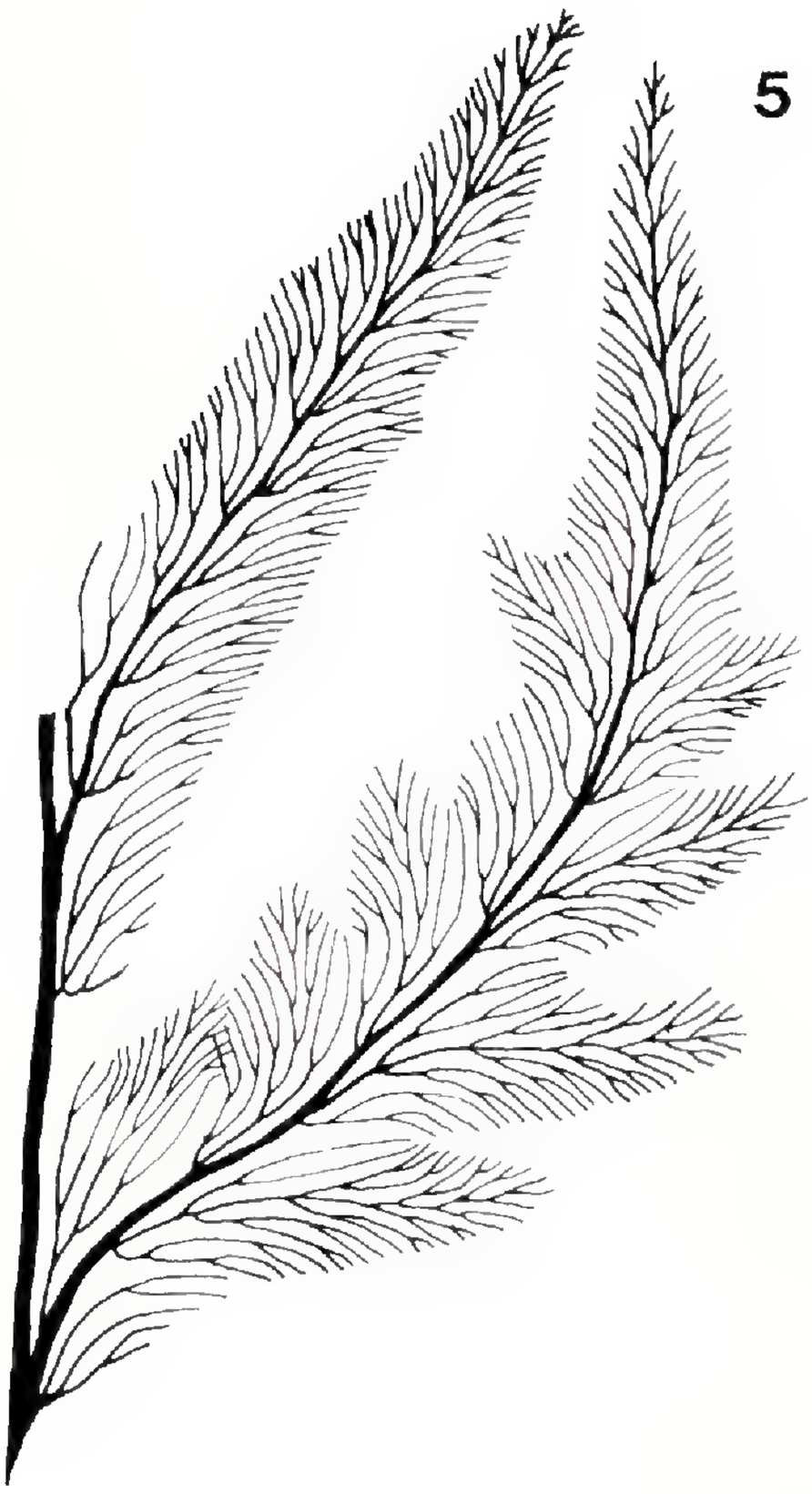
FIGURES 5–8. Leaf venation patterns in **Bommeria** species, × 2, drawn from material grown under uniform conditions: 5, *B. pedata*; 6, *B. hispida*; 7, *B. ehrenbergiana*; 8, *B. ehrenbergiana* × *hispida*.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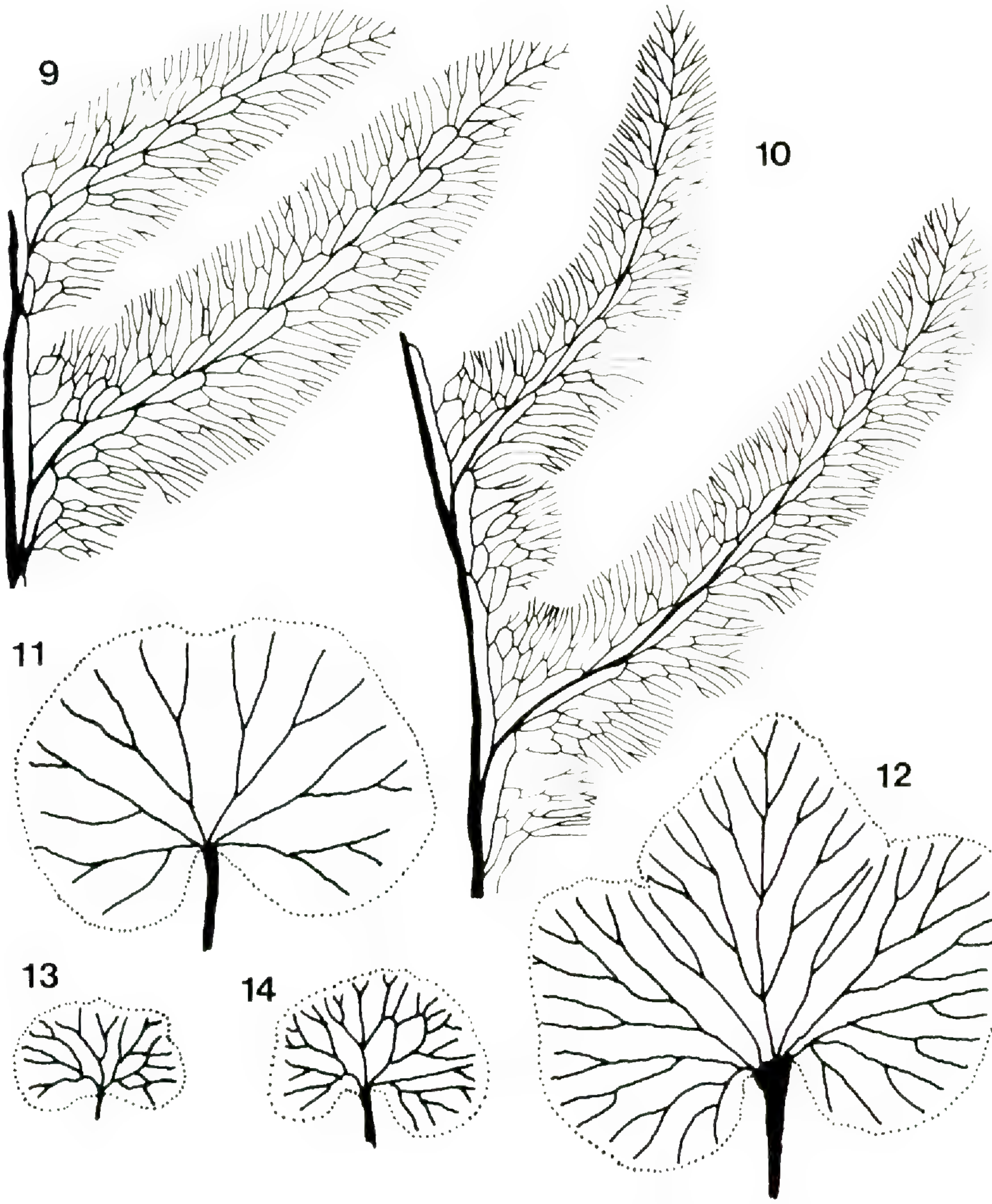
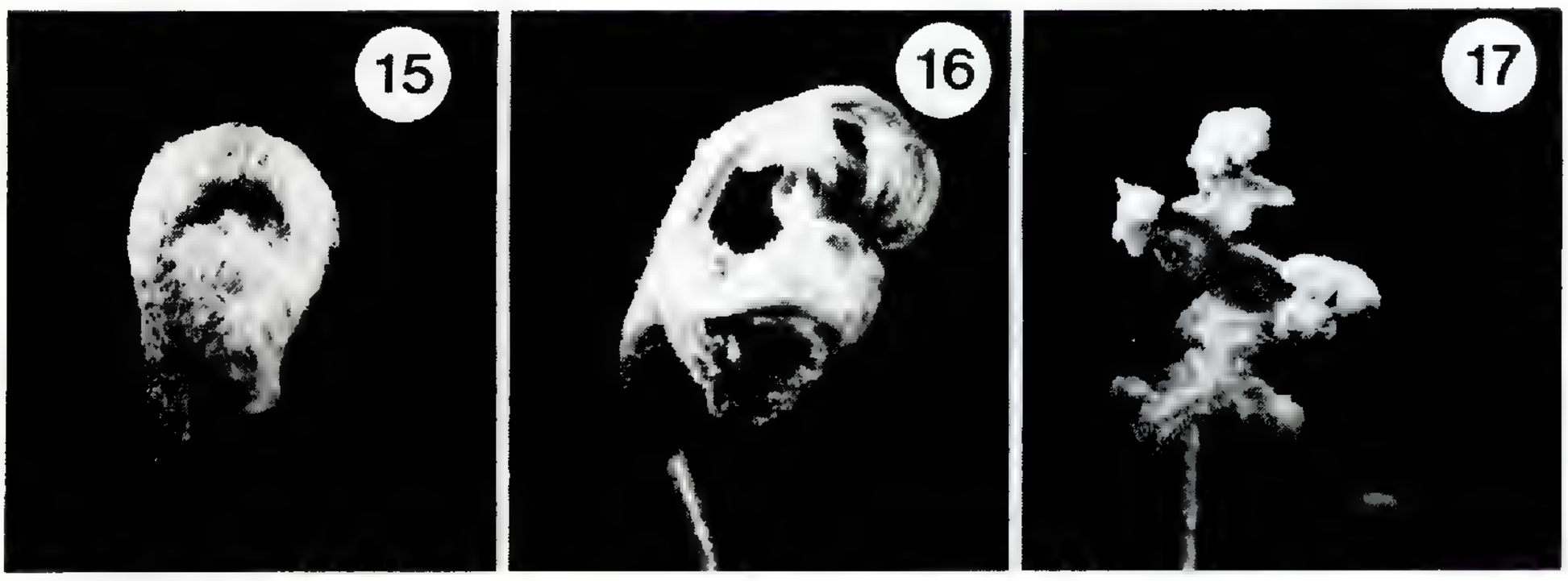


FIGURES 9–14. Leaf venation patterns in **Bommeria** species drawn from material grown under uniform conditions: 9, *B. subpaleacea*, × 2, from eastern Mexico; 10, *B. subpaleacea*, × 2, from Chihuahua; 11–14, heteroblastic series in leaves of *Bommeria* species, × 5; 11, 12, typical free-veined species, *B. pedata*; 13, 14, typical net-veined species, *B. subpaleacea*.

(1975) has reinterpreted *Botrychium* to be characteristically circinate because of the arrangement of the final leaf division. In work with a group more closely allied to *Bommeria*, Knobloch (1965) considered the buds of some *Cheilanthes* species to be noncircinate. Evidence from *Bommeria* suggests that vernation in these species might be better termed "partially circinate." In both *Cheilanthes* and *Bommeria*, although the leaf bud is originally "bent" (FIGURE 15), after extension of the bent portion (FIGURE 16), all segments of the leaf are circinately arranged (FIGURE 17).



FIGURES 15–17. Stages in leaf opening in **Bommeria** species, all × 3: 15, initial bent configuration (*B. pedata*); 16, crozier unbending (*B. ehrenbergiana*); 17, circinately arranged segments uncoiling (*B. ehrenbergiana*).

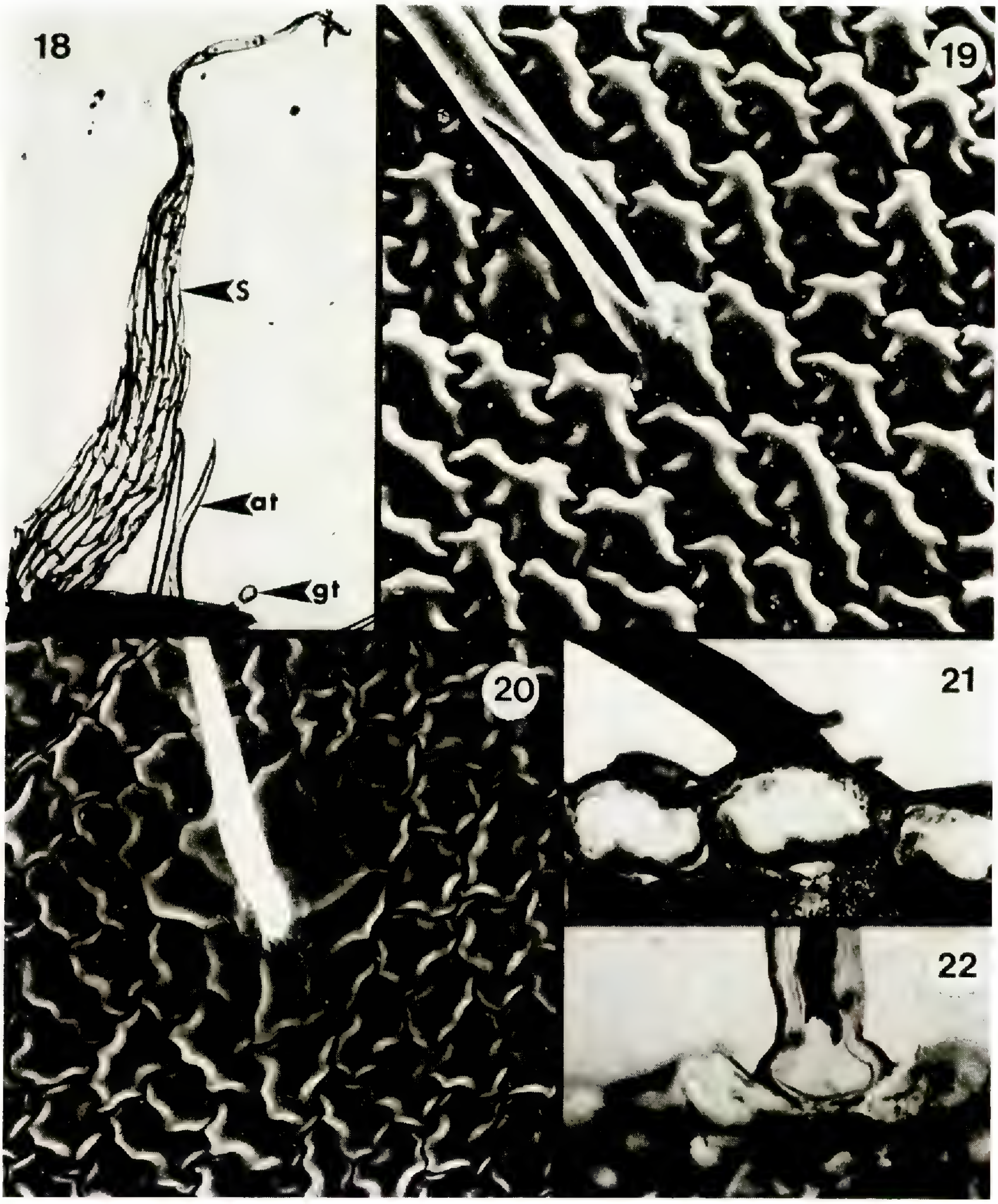
This arrangement seems to be only a mild departure from the typical condition and should not be termed noncircinate.

Indument. All species have tiny, glandular trichomes on their abaxial lamina surfaces early in leaf ontogeny (FIGURE 18). These dessicate and generally are absent by the time mature sporangia appear.

Unicellular, acicular trichomes are present on the abaxial lamina surface of all species, but the cell arrangement at the base of these trichomes in *Bommeria hispida* differs from that in the other species. In *B. hispida,* the trichomes arise from cells that are identical to neighboring epidermal cells and that are not sunken into the epidermal surface (FIGURES 19, 21); in other members of the genus, they arise from cells that are sunken into the epidermis and are surrounded by a radiating array of modified epidermal cells (FIGURES 20, 22). Acicular trichomes are also found on the abaxial lamina surfaces in all species, but there is no specialization of epidermal cells at the base of these trichomes. While acicular trichomes on both leaf surfaces show considerable variation in length (0.21 mm.–1.12 mm.), those of the adaxial surface are generally shorter (mean = 0.40 mm.) than those of the abaxial surface (mean = 0.70 mm.). Interspecific comparisons of acicular trichome length show that the trichomes of *B. hispida* are generally longer (mean adaxial length = 0.54 mm., mean abaxial length = 1.00 mm.) than those of its congeners (mean adaxial length = 0.36 mm., mean abaxial length = 0.63 mm.), but the extreme variability in trichome lengths precludes their use in taxonomic determinations.

Coiled, hygroscopic trichomes occur in *Bommeria* only on the abaxial leaf surfaces of *B. hispida.* This indument feature may act to protect the developing sporangia, and the hygroscopic movements of the trichomes may facilitate release of spores that would otherwise be trapped among the trichomes. These trichomes are difficult to measure because of their coiled nature, but they all appear to be between 1 and 2 mm. in length.

Scales are present on the leaves of all *Bommeria* species (FIGURE 18), but the morphology of these scales presents no stable interspecific varia-



FIGURES 18–22. Morphology of indument and associated structures in **Bomeria** species. 18, light micrograph of *B. hispida* showing multicellular scale (s), acicular trichome (at), and glandular trichome (gt), × 40. 19, 20, scanning electron micrographs: 19, *B. hispida*, adaxial trichome, showing lack of special basal cell arrangement, × 250; 20, *B. subpaleacea*, showing rosette of basal cells associated with adaxial trichome, × 190. 21, 22, adaxial trichome bases, sectional view, × 300: 21, *B. hispida*; 22, *B. ehrenbergiana*.

tion. The greatest variation is on leaf buds: the largest scales, which may develop thickened "mid-rib" regions, are the most superficial; the scales become gradually diminished in size and complexity in moving from the outer bud indument toward the epidermal surface of the bud, where they are small and uniseriate. Bud scales probably function most importantly

in protecting the developing bud against dessication and mechanical injury. The taxonomic usefulness of scale morphology is limited by the extreme variability within individuals and by the lack of such distinctive structural features as glandular tips or hispid margins. The distribution of scales on mature leaves, however, offers consistent interspecific differences. In *B. ehrenbergiana* and *B. pedata*, scales are few or lacking on the abaxial lamina surface, and any scales that are present are never more than 8 cells wide at the base. In *B. hispida* and *B. subpaleacea*, scales are conspicuous on the abaxial lamina surface and are commonly 10 or more cells wide at the base.

Sporangial arrangement. The sporangia in all *Bommeria* species are borne along the veins over much of the abaxial lamina surface and have no protective indusia. In *B. ehrenbergiana*, the sporangia are more restricted to the margins than they are in other members of the genus and cover only a quarter to a third of the distance from the lamina margin to the costa of each ultimate segment.

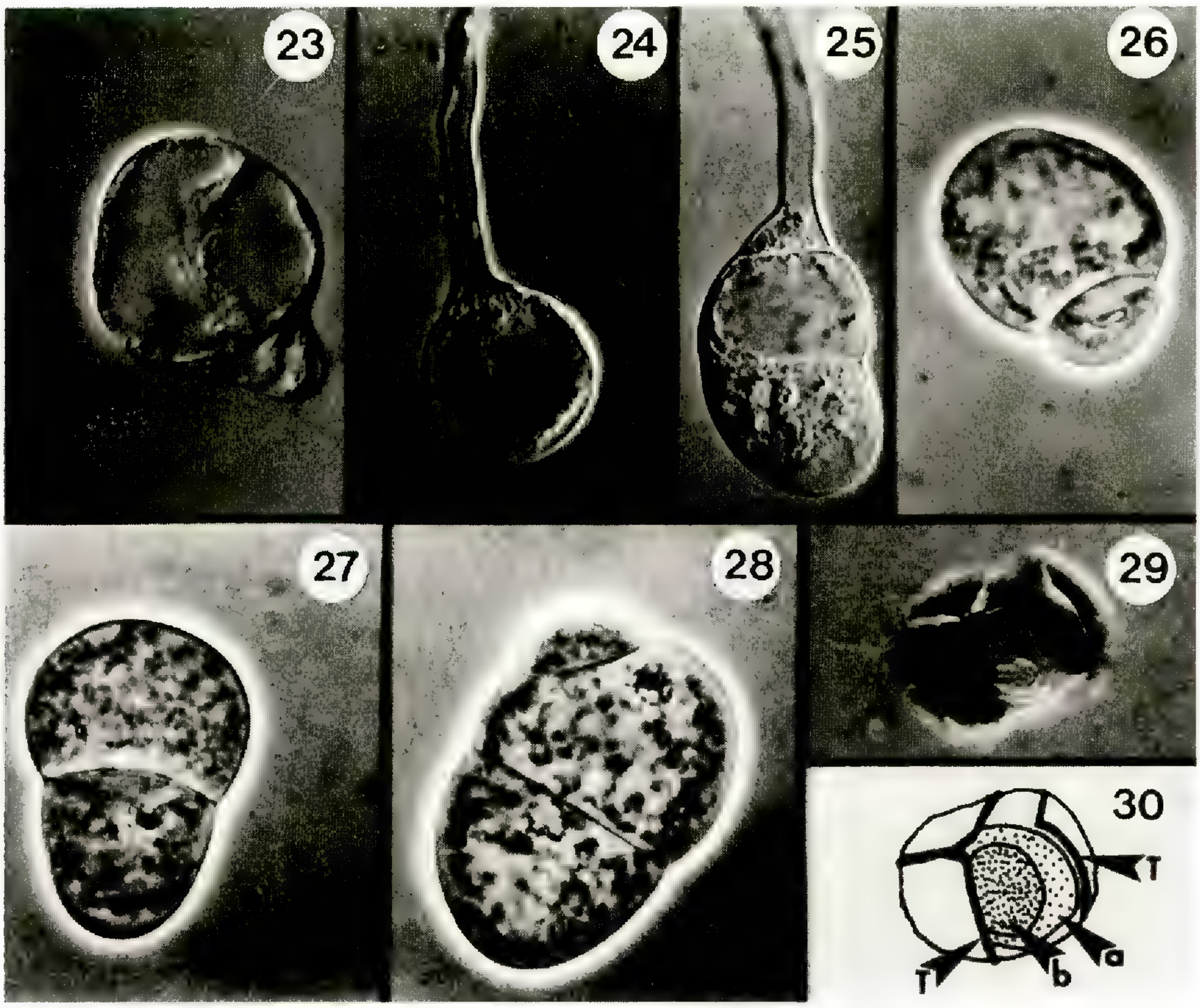
Gametophyte Ontogeny and Morphology

Aspects of gametophyte ontogeny relevant to breeding system analysis have been discussed elsewhere (Haufler & Gastony, 1978a). Further features of gametophyte morphology and ontogeny are presented here. Other workers (see Nayar & Kaur, 1971, for review) have found two aspects of vegetative gametophyte development to be valuable in discussions of fern classification: the orientations of the initial divisions of the germinating spore, and the position and configuration of the meristem. Gametophyte ontogeny presented here concentrates on the characteristics of these two aspects in *Bommeria*.

Among *Bommeria* species, gametophytes develop at two different rates. Morphological features (e.g., type of lobing, meristem configuration) are similar among all species, but such features appear earlier in gametophytes of *B. pedata*, the triploid apomict, than in those of the sexual species. Developmental stages discussed below are cited as they occur in days elapsed from the time of spore sowing. The times for *B. pedata* are placed in parentheses following the listing for the sexual species.

Spores of *Bommeria* species germinate 4 to 7 (3 to 5) days after sowing. The first evidence of germination is the cracking of the spore wall along the lines of the tri-radiate ridge. At this time, there are generally two cells present within the spore wall (Figures 23, 26). The first division is nearly perpendicular to the polar axis of the spore (Figures 29, 30). In most species of *Bommeria* examined, the smaller of these initial cells becomes a rhizoid (Figure 24); however, in *B. subpaleacea* the smaller cell frequently enlarges and becomes a prothallial cell. The first rhizoid, although apparently derived from the same cell as the prothallial cell, appears as the third cell of the gametophyte (Figures 26–28).

Gametophyte growth between spore germination and meristem formation produces a haphazard, irregularly lobed thallus in *Bommeria* (Fig-

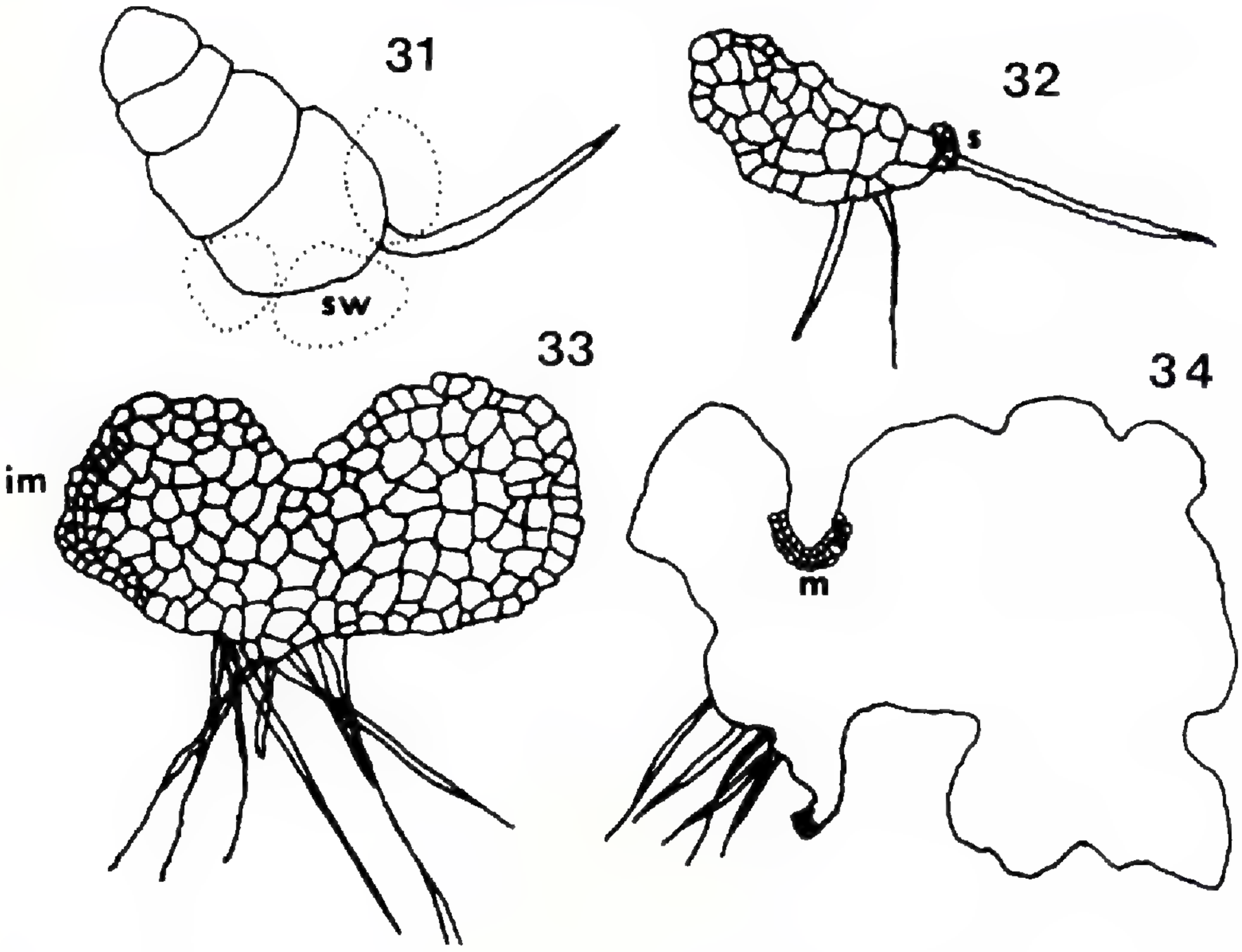


FIGURES 23–30. Initial cell divisions in gametophytes of **Bommeria** species. 23–25, most common division series with first cell division producing a rhizoid. 26–28, division series found in some *B. subpaleacea* gametophytes, in which first cell division produces a prothallial cell. 29, 30, photograph and interpretive drawing of early two-celled gametophyte (with spore wall still intact) to show orientation of first division with respect to spore axes. First division perpendicular to polar axis. 23–25, *B. hispida*; 26–30, *B. subpaleacea*. 23–25, 29, interference-contrast optics; 26–28, phase-contrast optics. 23, 25–28, × 500; 24, 29, 30, × 400. Abbreviations: T = trilete scar on spore wall; a = original cell of gametophyte; b = cell formed by first division.

URES 31–34). The meristem is initiated laterally in all species following 20 to 23 (13 to 15) days of growth (FIGURES 33, 34). Soon after initiation of the *Ceratopteris*-type (multicellular) meristem (terminology *sensu* Nayar & Kaur, 1969), a distinct meristematic notch is formed (FIGURE 34). Although the meristem forms a notch region, *Bommeria* species never form symmetrically cordate gametophytes. Instead, they become increasingly irregular in their lobe formation, often having projections that extend as 1- or 2-cell-wide straps of tissue away from the main prothallial body.

EXPERIMENTAL HYBRIDIZATION

Crosses were attempted between all possible species pairs in *Bommeria*, and intergenerically between *Hemionitis palmata* L. and *B. hispida* and *B.*



FIGURES 31–34. Camera lucida drawings of typical stages in gametophyte development of **Bommeria** species: 31, *B. ehrenbergiana*, 7 days after sowing, × 250; 32, *B. subpaleacea*, 14 days after sowing, × 100; 33, *B. subpaleacea*, 21 days after sowing, × 60; 34, *B. hispida*, 28 days after sowing, × 25. Abbreviations: im = immature meristem; m = meristem; s = spore remnants; sw = spore wall.

subpaleacea. Although crossing data may not be of ultimate importance in defining plant species (see Raven, 1976, for discussion), they may be appropriately applied in combination with other characters in establishing natural groups. Given the antheridiogen-controlled breeding system (Haufler & Gastony, 1978a), artificial crosses between individuals of *Bommeria* species should be relatively straightforward. The paucity of sperm-releasing antheridia in most cultures, however, decreased the facility with which hybridization could be accomplished. Gametophytes often produce abundant antheridia, but many of these gametangia fail to release active sperm. In addition, even when sperm is active and plentiful, intraspecific fertilization controls, initiated concomitantly with the interspecific cross attempts, failed to form sporophytes. Thus, conclusions cannot be based on the failure of an interspecific cross; only the actual formation of a sporophyte and the subsequent analysis of its morphological and cytological characteristics bear on discussions of interspecific relationships.

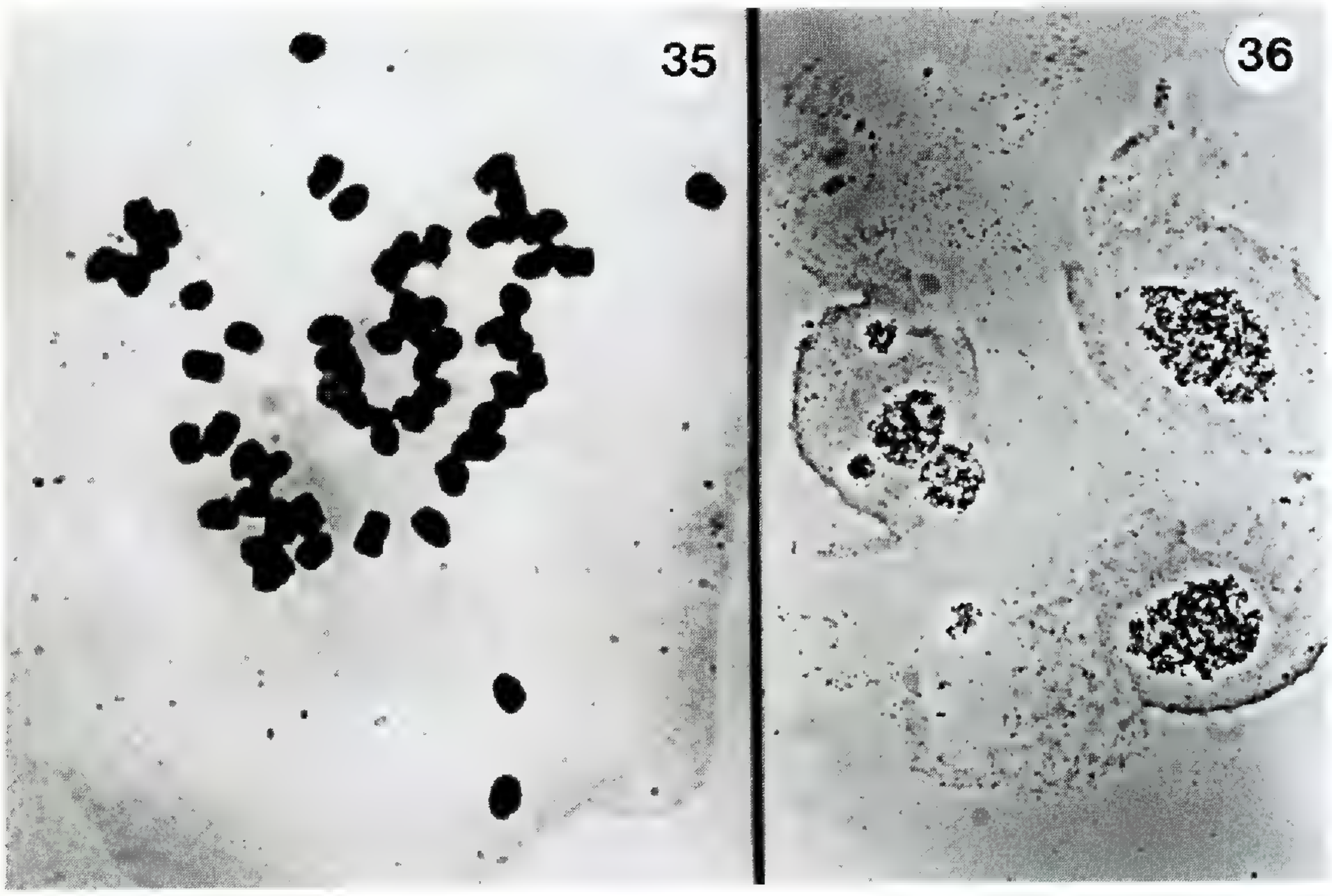
Three crosses provide data relating to the consistency of disjunct intraspecific populations and the genetic discontinuity between species. The first two (*Bommeria hispida*, Texas, *Haufler & Haufler 1* (IND) × *B. hispida*, New Mexico, *Haufler & Haufler 7* (IND); *B. hispida*, Arizona,

Haufler & Haufler 5 (IND) × *B. hispida*, Jalisco, *Gastony & Haufler 1073* (IND)) produced vigorous sporophytes having regular chromosome pairing during meiosis and well-formed, viable spores. Crosses between neighboring and widely separated populations indicate significant uniformity in the genetic constitution of *Bommeria hispida* throughout its range and suggest that there are no chromosomal or genetic barriers to interpopulational gene flow.

The third cross (*Bommeria hispida*, Texas, *Haufler & Haufler 3* (IND) × *B. ehrenbergiana*, Hidalgo, *Gastony & Haufler 1086* (IND)) produced a vigorous but sterile hybrid that is intermediate in the differing parental characters (TABLE 1). All mature sporangia were shrunken and had aborted contents. Analysis of sporogenesis revealed general meiotic breakdown. At diakinesis there were 60 univalents (FIGURE 35), indicating complete lack of bivalent formation. Early tetrad formation was characterized by the presence of chromatin fragments (FIGURE 36). Although there are many obvious morphological differences between *Bommeria hispida* and *B. ehrenbergiana* (TABLE 1), there is insufficient genetic differentiation between these species to preclude production of a vegetatively vigorous hybrid. The success of this cross has implications at interspecific and intergeneric levels. The fact that a hybrid has been successfully produced between these two very distinctive species suggests that it may be possible to make interspecific crosses between any of the species within

TABLE 1. **Comparison of the parental species and the hybrid derivative of a cross between Bommeria hispida and B. ehrenbergiana.**

	B. hispida	*B. ehrenbergiana*	Hybrid
LEAF SIZE	Small (blade 35–55 mm. long)	Large (blade 100–150 mm. long)	Intermediate (blade 65–85 mm. long)
VENATION	Free	Anastomosing	Some anastomoses occasionally present
ABAXIAL TRICHOMES	Acicular and coiled	Only acicular	Predominantly acicular with a few coiled ones present
ADAXIAL TRICHOME BASE	Unspecialized	With special radiating cells	Both types present
SPORANGIA	Covering much of abaxial leaf surface	Restricted to leaf margins	Somewhat restricted to leaf margins
SCALES	Common on abaxial leaf surface	Few or absent on abaxial leaf surface	Present on main veins but uncommon on leaf surface



FIGURES 35, 36. Stages in meiosis of **Bommeria ehrenbergiana** × **hispida**: 35, diakinesis showing 60 univalents, × 1500; 36, products of irregular meiotic divisions of a single spore mother cell, × 1000 (note micronuclei and presence of only three major products of these meiotic divisions).

Bommeria. Within the tri-generic complex consisting of *Bommeria, Hemionitis*, and *Gymnopteris*, there often appear to be greater differences between the species of a single genus than between those of different genera. One might therefore expect intergeneric crosses to be as easy as intrageneric ones. Mickel (1974) reported the discovery in nature of a sterile hybrid apparently resulting from a cross between *Gymnopteris rufa* (L.) Bernh. and *Hemionitis palmata* L., but the present crossing program failed to form successful intergeneric hybrids.

Although valuable information concerning relationships among *Bommeria* species could be obtained from the successful production of sporophytes from any interspecific hybridization, perhaps the most pertinent cross would be one between Chihuahuan and other populations of *B. subpaleacea*. All lines of evidence indicate that individuals from these isolated Chihuahuan populations (previously referred to *B. knoblochii*) do not differ significantly from other *B. subpaleacea* populations. Thus, one might expect crosses between these populations to yield sporophytes. Many crosses were attempted between Chihuahuan and other populations of *B. subpaleacea*, but no sporophytes ever developed. These attempts included instances in which every stage in the process, from release of active sperm to the swimming of sperm down a receptive archegonial neck, was microscopically monitored. Although these crossing failures suggest that there are barriers to hybridization between these populations, the difficulty encountered in obtaining sporophytes in numerous intrapopulational fertilizations

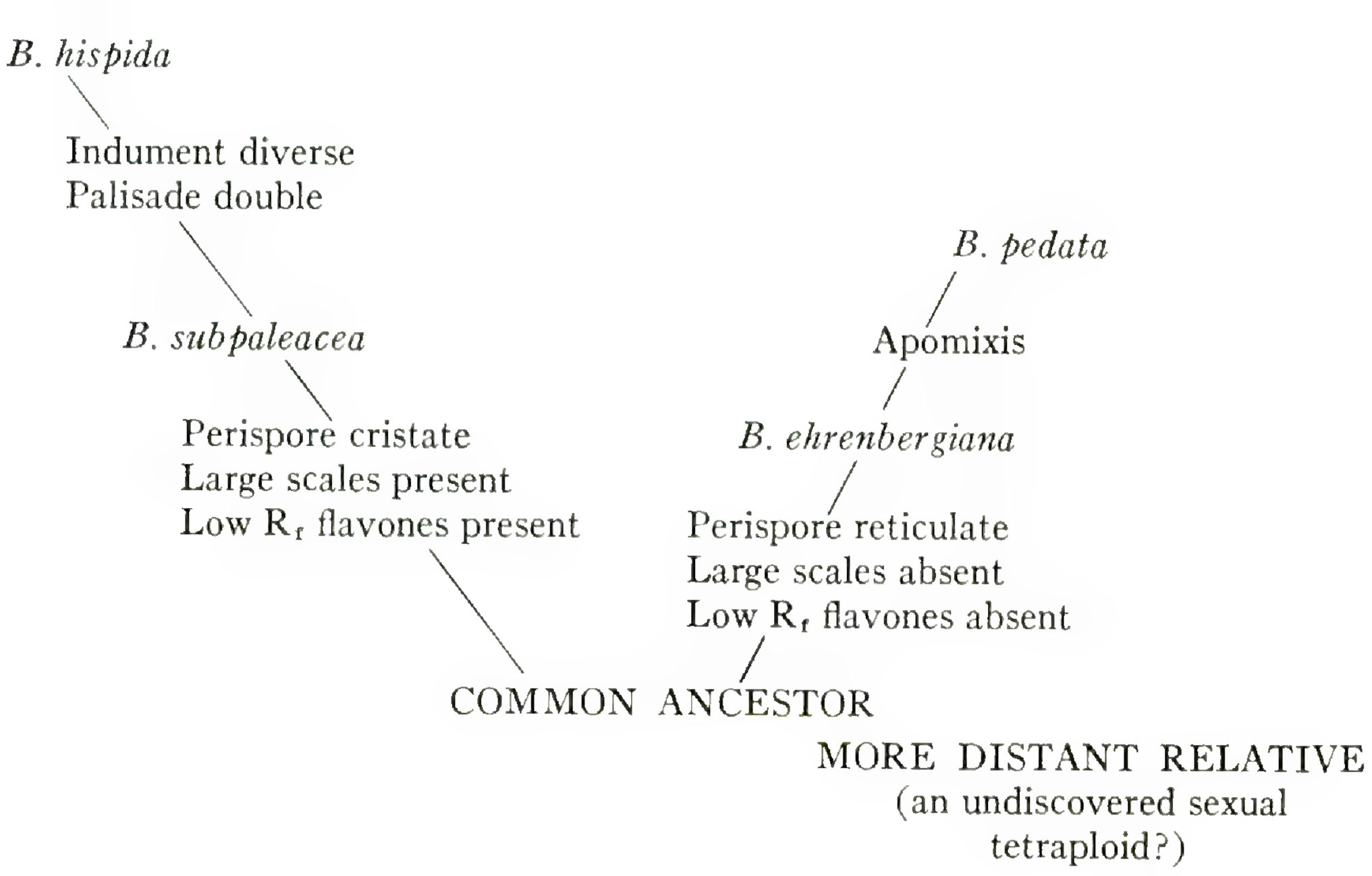
(especially from Chihuahua) renders this lack of interpopulational hybrids less significant.

DISCUSSION

EVOLUTIONARY TRENDS AND BIOGEOGRAPHY

All of the data presented indicate that *Bommeria* species are clearly related to one another, but detection of phylogenetic relationships is complicated since most gametophyte and sporophyte characteristics are either uniform throughout the genus or fail to correlate with each other in establishment of infrageneric groups (TABLE 2). Spore, scale, and chemical data, however, do correlate and suggest a basic dichotomy among the species. *Bommeria hispida* and *B. subpaleacea* share cristate spores, conspicuous scales on their abaxial leaf surfaces, and flavones with low R_f values. In contrast, *B. pedata* and *B. ehrenbergiana* have reticulate spores, lack large scales on their leaves, and do not have low R_f flavones.

Thus, the following phylogeny is suggested:

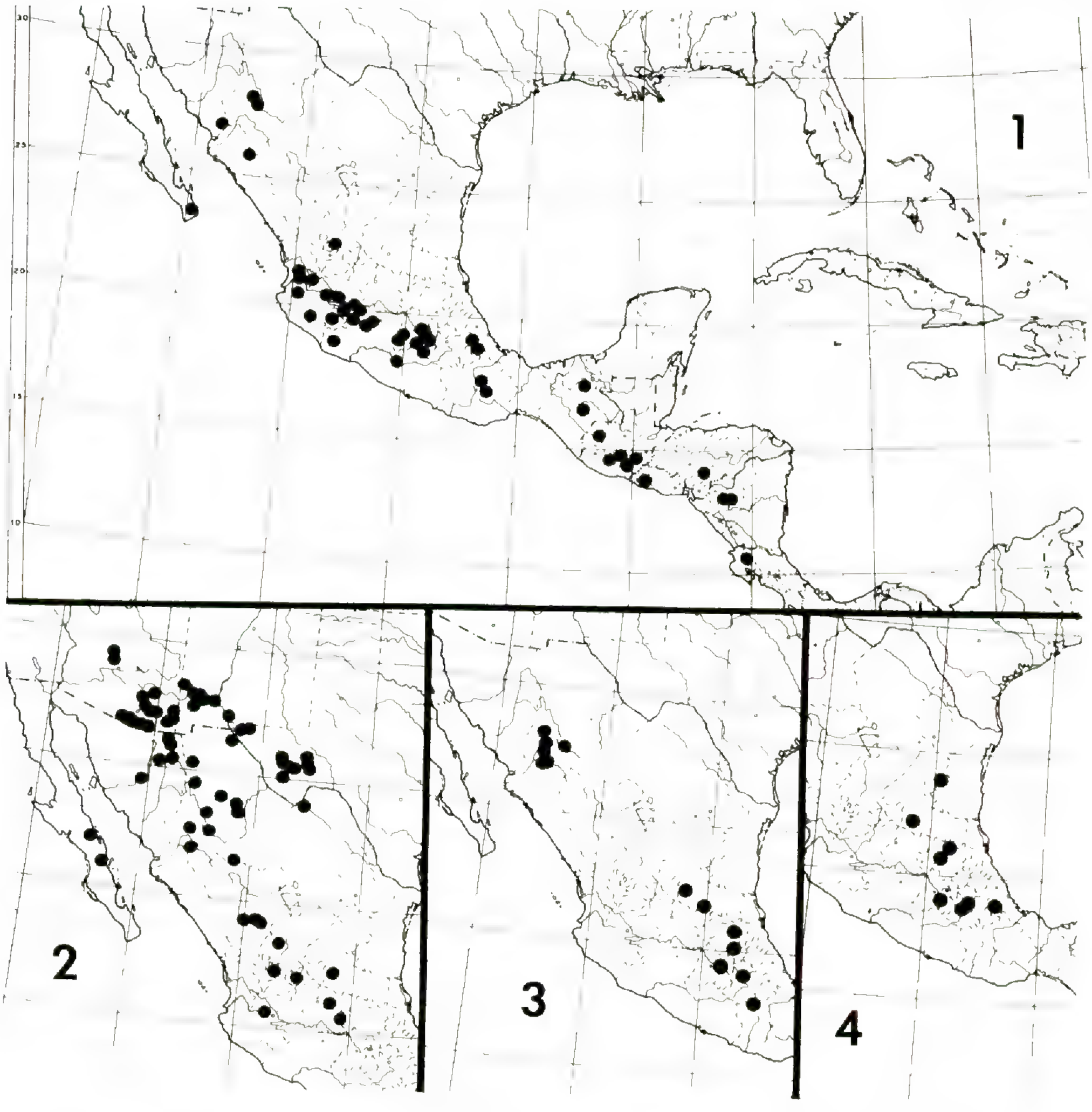


Bommeria hispida, with its specialized leaf anatomy (double palisade layer), diverse indument (presence of both acicular and coiled trichomes), and creeping rhizome, is the most distinctive and derived member of the genus. Based on its geographic range (MAP 2), *B. hispida* is the most successful sexual species. The xeric adaptations of the sporophyte of *B. hispida* (small, well-dissected leaves with extensive indument) apparently enable it to withstand greater environmental stress than can the other species. It is the only species, for example, found in areas characterized by subfreezing temperatures. Although the Chihuahuan populations of *B. subpaleacea* are in a region that experiences snow during winter months,

TABLE 2. Summary of interspecific variation in sporophyte structures of Bommeria.

	RHIZOME	LEAF																
	Internode length (mm.)		Mean blade length (mm.)			Rachis		Lobe apex		Palisade layer thickness (# cells)		Venation		Adaxial trichome base		Abaxial trichome types		Abaxial scale distribution		Sporangial distribution	
SPECIES	7–10	0.5–1.5	40	60–85	100	Cast.*	Atro.†	Round	Acute	2 or 3	0–2	Free	Areolate	Simple	Specialized	Acicular	Acicular & coiled	Dense	Sparse	Marginal	Not marginal
B. hispida	+		+			+		+		+		+		+			+	+			+
B. ehrenbergiana		+		+			+	+			+		+		+	+			+	+	
B. pedata		+		+		+			+		+	+			+				+		+
B. subpaleacea (eastern Mexico and Chihuahuan collections)		+		+		+		+	+		+		+		+			+			+

* Cast. = castaneous.
† Atro. = atropurpureous.



MAPS 1–4. Distribution of **Bommeria** species as documented by herbarium specimen data: 1, *B. pedata*; 2, *B. hispida* (disjunct collection from Nicaragua not plotted); 3, *B. subpaleacea*; 4, *B. ehrenbergiana*.

these plants are found only in moist canyons at low elevations where temperatures never fall below freezing.

Analysis of herbarium specimens indicates that *Bommeria pedata* is morphologically uniform throughout its range and has 32-spored sporangia in all populations; thus, this species is consistently apomictic. The above phylogeny indicates *B. ehrenbergiana* as the most likely species within *Bommeria* to have served as one of the progenitors of this hybrid-derived, apogamous triploid. One of the major differences between *B. ehrenbergiana* and *B. pedata* is that the veins of the former are anastomosing, while those of the latter are free. The diploid-diploid cross between the net-veined *B. ehrenbergiana* and the free-veined *B. hispida* (discussed above) resulted in a hybrid having very few anastomoses (FIGURE 8). If the diploid *B. ehrenbergiana* were crossed with a free-veined tetraploid, the tetraploid characteristics would most likely predominate and could yield a free-veined

hybrid. Based on currently available cytological and morphological data, there are no candidates within *Bommeria* or among those taxa closely related to the genus that could be the tetraploid parent, but the chromosome numbers of many species are still unknown. *Bommeria pedata* may also have arisen *de novo* through hybridization between diploid and tetraploid populations of a now extinct species or via production of unreduced gametes in a diploid population. Until *B. pedata* is synthesized, however, all such explanations remain hypothetical.

Bommeria pedata reproduces asexually and so is not limited by the breeding system that characterizes the sexual *Bommeria* species and that requires the presence of at least two gametophytes to produce a new sporophyte (Haufler & Gastony, 1978a). This apomict is therefore the only *Bommeria* species capable of single spore migration. Probably because of this adaptation, *B. pedata* has an extensive range, but it is not found in regions experiencing subfreezing temperatures. Whereas the gametophyte generation limits range extension of the sexual species, it appears that the sporophyte of *B. pedata* restricts this species to tropical and subtropical climes.

The environmental requirements and breeding system of *Bommeria subpaleacea* and *B. ehrenbergiana* appear to be instrumental in determining their restricted distributions. Sporophytes of these species do not have the xeric adaptations that characterize *B. hispida*; their foliage does not survive even brief dry periods. Their gametophytes lack the advantages seen in *B. pedata* of rapid development and apogamous sporophyte initiation; *B. subpaleacea* and *B. ehrenbergiana* gametophytes develop slowly and require free water for fertilization. Furthermore, the antheridiogen-controlled gametophytic breeding system (Haufler & Gastony, 1978a) hampers migration, and thus range extension, since at least two spores must travel, germinate, and produce juxtaposed gametophytes to form each of the two gametangia and thus reproduce sporophytes. *Bommeria subpaleacea* and *B. ehrenbergiana* are unable to survive on the mountains or in the deserts, which separate their mesic canyon sanctuaries, and their ability to migrate is severely limited by their breeding system. They therefore remain as Mexican endemics with very restricted ranges.

Intergeneric Relationships

In gymnogrammoid and cheilanthoid ferns there are often more clearly defined differences between species within a genus than there are between genera. Although the present study of *Bommeria* explores the reproductive biology and taxonomy of all members of the genus as presently defined, the confused and perhaps artificial boundaries among the genera related to *Bommeria* limit the application of these data in discussions of generic and suprageneric species groups.

Species characters in *Bommeria* suggest that members of this genus may be a pivotal assemblage in the classification of gymnogrammoid and cheilanthoid ferns. In the following paragraphs, evidence derived from a

variety of characters and life cycle stages are presented and related to the definition of natural species groups.

The presence or absence of scales, for example, has been used to separate gymnogrammoid genera. Copeland (1947) segregated *Paraceterach* Copel. from *Gymnopteris* because of the abundance of scales in the former genus and their scarcity in the latter. *Bommeria* species have an intermediate scale abundance and may thus provide a link between species primarily having trichomes and those with an extensive scale complement.

Aspects of spore morphology and sporangial distribution suggest that *Bommeria ehrenbergiana* and *B. pedata* may demonstrate a close relationship between the cheilanthoid and gymnogrammoid groups. Although more survey work is necessary, presently available data indicate that these two species are unique among gymnogrammoid ferns in having a reticulate perispore topography (Haufler & Gastony, 1978b), a spore type commonly associated with cheilanthoid genera (Tryon & Tryon, 1973; Quirk & Chambers, 1978). The distribution of sporangia, which are marginally restricted in cheilanthoid ferns and cover much of the abaxial leaf surface in gymnogrammoid ferns, is often stressed as an important character in delimiting these two groups. The somewhat marginally distributed sporangia characteristic of *B. ehrenbergiana* and occasionally encountered in *B. pedata* correlate with the foregoing perispore features to support the intermediate status of these *Bommeria* species.

Pedate leaf architecture, universal in *Bommeria*, is also scattered among the species of other genera, appearing in the gymnogrammoid genera *Hemionitis* and *Pityrogramma* Link and in the cheilanthoid genera *Doryopteris* and *Notholaena* R. Br. The somewhat random occurrence of this character, perhaps a manifestation of convergent evolution, suggests that the importance of leaf architecture in defining generic boundaries should be deemphasized. The work of Mickel (1974) shows that leaf architecture is not useful in defining *Hemionitis* and *Gymnopteris* as genera.

Gametophyte development in gymnogrammoid ferns has not been extensively studied, but the limited work that has been done with the gametophytes of *Hemionitis*, *Gymnopteris*, and *Bommeria* indicates that characteristics of this stage of the life cycle may be significant in generic definition. *Bommeria* has a *Ceratopteris*-type (multicellular) meristem and is assymetrically cordate, i.e., has unequal-sized lobes flanking the meristematic notch. Nayar (1956) showed that the gametophyte of *Hemionitis arifolia* (Burman) Moore has an *Adiantum*-type (unicellular) meristem and is symmetrically cordate at maturity. Kaur (1972) described gametophyte development in *Gymnopteris vestita* (Wall.) Underw. as differing slightly from that in *H. arifolia*. A symmetrically cordate mature gametophyte is formed, but, among the gametophytes studied, the meristem varied from single-celled in some prothalli to multicellular in others. More exacting and complete work with the gametophytes of *Hemionitis* and *Gymnopteris* species is necessary before any conclusions can be drawn, but existing evidence suggests that there is variation in gametophyte on-

togeny and morphology and that careful analysis of this variation may be valuable in assessing intergeneric alliances.

Although the gametophyte characters discussed above may be valuable in generic distinctions, evidence from study of gametophyte development in *Bommeria* and other genera suggests that the taxonomic significance of the pattern of cell divisions during spore germination may be overstated. Nayar and Kaur (1971) cite evidence predicting that the plane of the first cell division in *Bommeria* and related genera should be perpendicular to the polar axis of the spore and that the first cell produced should be a rhizoid. In *B. subpaleacea*, gametophytes grown from a single spore source exhibit two developmental types: the first cell formed may differentiate into either a rhizoid or a prothallial cell. Endress (1974) demonstrated a similar departure from the Nayar and Kaur scheme in gametophytes of *Ceratopteris* Brongn., the first cell of which is always prothallial. Baroutsis (1976) showed that the plane of the first division in *Anogramma* Link gametophytes is parallel to the polar axis. Although Nayar and Kaur (1971) predict that all of these genera should have the same pattern of development, the studies discussed here question the stability of early gametophyte development stages in establishing natural species groupings.

As stated earlier, *Bommeria* has been most commonly allied with *Hemionitis* and *Gymnopteris*. The data presented here, however, emphasize the unsettled nature of the generic affinities of *Bommeria*. Although the genus clearly has characters that associate it with the gymnogrammoid ferns, it has other features that show a close relationship with the cheilanthoid group. The present study, in conjunction with others (see, for example, Giannasi, 1974; Tryon & Tryon, 1973; Nayar & Kaur, 1971), has introduced the application of three lines of evidence — flavonoid chemistry, spore morphology, and gametophyte ontogeny — that may prove valuable in the delimitation of gymnogrammoid and cheilanthoid genera. Extensive application of these techniques to other genera is necessary before more natural groups become evident. It is hoped that the data accumulated and discussed in relation to *Bommeria* may be integrated with data from future investigations to enable a better understanding of the phylogenetic relationships among the cheilanthoid and gymnogrammoid ferns.

TAXONOMIC TREATMENT

Bommeria Fourn. in Baillon, Dict. Bot. 448. 1876. LECTOTYPE: *Bommeria ehrenbergiana* (Kl.) Underw. (*Gymnogramma ehrenbergiana* Kl.), chosen by Maxon, Contr. U. S. Natl. Herb. 17: 168. 1913.

Rhizome prostrate, short, and seldom branched to long-creeping and often branched, solenostelic to dictyostelic, indument of scales and unicellular, sometimes coiled, trichomes. Petiole castaneous to atropurpureous, terete to sulcate, indument of scales and (or) trichomes especially at base

and apex. Lamina pentagonal, pedate, composed of three segments (one apical and two basal), 1–16 cm. in length, usually about as wide as long; apical segment pinnatifid in distal portion, pinnatifid to bipinnatifid in basal portion; basal segments usually connected to apical by narrow wing along rachis, inequilaterally elongate-deltoid, lowest basiscopic portion much elongated and pinnatifid to bipinnatifid; ultimate segments acute to rounded at apex; adaxial indument of unicellular, acicular trichomes with or without specialized basal cells, abaxial indument of scales, unicellular, coiled trichomes, and unicellular, acicular trichomes; rachis castaneous to atropurpureous; venation open to areolate. Sporangia borne along the veins, covering much of the abaxial leaf surface or somewhat marginally restricted, indusium absent. Spores 32 or 64 per sporangium, globose with smooth exospore and cristate or reticulate perispore surfaces. Gametophytes unisexual; archegonial, assymetrically cordate with multicellular meristem; antheridial, spatulate and ameristic.

KEY TO THE SPECIES OF BOMMERIA

1. Venation open.
   2. Rhizome long-creeping, the leaves borne at 7–10 mm. intervals; leaves with apex of ultimate segments rounded, abaxial trichomes dimorphic, abaxial scales commonly with 10 or more cells across the base; sporangia with 64 spores, abortive ones absent. ..... 1. *B. hispida.*
   2. Rhizome short, the leaves borne at ca. 1 mm. intervals; leaves with apex of ultimate segments acute, abaxial trichomes monomorphic, abaxial scales with 2 to 8 cells across the base; sporangia with 32 spores, abortive ones also frequent. ..... 2. *B. pedata.*
1. Venation areolate.
   3. Scales on abaxial leaf surface commonly with 10 or more cells across base; rachis wholly castaneous; ultimate segments with fertile veins extending ⅔–¾ of distance from margin to costa. ..... 3. *B. subpaleacea.*
   3. Scales on abaxial leaf surface with 2 to 8 cells across base; rachis atropurpureous, ½–⅔ length of lamina; ultimate segments with the fertile veins extending ¼–½ of distance from margin to costa. ..... 4. *B. ehrenbergiana.*

1. Bommeria hispida (Kuhn) Underw. Bull. Torrey Bot. Club **29:** 633. 1902. FIGURE 37; MAP 2.

Gymnogramma hispida Kuhn, Linnaea **36:** 72. 1869. TYPE: United States, Texas, Pass of the Limpia, crevice of rocks on the mountains, August 25, 1849, *Wright 819* (holotype, B, *n.v.*; isotypes, GH!, MO!, NY!, US!, YU!).

Neurogramme hispida (Kuhn) Diels in Engler & Prantl, Nat. Pflanzenfam. **1**(4): 264. 1899.

Gymnopteris hispida (Kuhn) Underw. Native Ferns. ed. 6. 84. 1900.

Bommeria schaffneri Fourn. Bull. Bot. Soc. France **27:** 327. 1880. TYPE: Mexico, in montibus Escabrillos prope San Luis Potosí, *Schaffner 6* (holotype, P, *n.v.*; isotypes, GH photo!, US photo!).

Gymnogramma schaffneri (Fourn.) Baker, Ann. Bot. **5:** 484. 1891.

Gymnogramma ehrenbergiana Klotzsch var. *muralis* Pringle ex Davenport,

Bot. Gaz. **19:** 392. 1894. TYPE: Mexico, Jalisco, on cliff faces near Tequila, July 6, 1893, *Pringle 4420* (holotype, GH!, ex Davenport Herb.; isotypes, F!, GH!, MEXU!, MSC!, TEX!, US! VT!).

Rhizome long-creeping and often branched, solenostelic, leaves arising at 0.7–1.0 cm. intervals. Petiole castaneous to atropurpureous, generally terete (but distally sulcate in some larger leaves), indument of scales at base, of scales and trichomes at apex, central portion generally glabrous. Lamina 1–7 cm. in length; ultimate segments rounded at apex; adaxial indument of unicellular, acicular trichomes (0.47–1.11 mm. in length) arising from unspecialized basal cells, abaxial indument of scales (commonly with 10 or more cells across the base), unicellular, acicular trichomes (0.75–1.12 mm. in length) and unicellular, coiled trichomes (ca. 1.0–2.0 mm. in length); rachis castaneous; venation open. Sporangia covering $\frac{2}{3}$–$\frac{3}{4}$ of the distance from the margin to the costa of each ultimate segment. Spores 64 per sporangium; perispore surface cristate.

DISTRIBUTION. Texas to California, United States; south through northern and central Mexico to Jalisco and San Luis Potosí; one disjunct collection from Nicaragua. Primarily in mountainous, xeric regions at altitudes of 1000 to 2500 meters, appearing as isolated plants at the base of boulders on steep, rocky hillsides, occasionally forming more extensive mats.

Bommeria hispida is the most morphologically and chemically distinct (Haufler & Giannasi, in prep.) of the species. Many of the characters that contribute to this uniqueness are those that may increase its xeric adaptiveness. Small leaf size, dissected segments, double palisade layer, and extensive and diverse indument are features that have been linked to high light–low humidity habitats (Shields, 1950) and may contribute to the success of *B. hispida* as evidenced by its extensive range (MAP 2).

There is one enigmatic collection of *Bommeria hispida* from Nicaragua (*L. Gómez P. 1055* (CR)!). Although this specimen is clearly *B. hispida*, it is about 1000 miles from the southernmost collection in Mexico. During field work in Jalisco, Mexico, I found *B. hispida* growing with *B. pedata*, a species that has been collected from many of the mountainous regions of southern Mexico, Guatemala, and Honduras. One might expect, therefore, that *B. hispida* would grow in these regions as well, but there are no reports of it between Mexico and Nicaragua. Perhaps future collections will fill in this large disjunction.

D. C. Eaton introduced confusion into the generic taxonomy when in 1883, without knowledge of Fournier's 1876 work, he combined *Gymnogramma hispida* with *G. ehrenbergiana*. Until that time, the two species were considered distinct since the venation of *G. hispida* is open and that of *G. ehrenbergiana* is areolate. Eaton evidently based his decision on an examination of the *Parry & Palmer 1006* collection, two sheets of which (YU and NY) have leaves of both *G. hispida* and a second species (now recognized as *B. subpaleacea*) that, because of its areolate venation, Eaton took to be *G. ehrenbergiana*. Eaton noted on the NY sheet that "both

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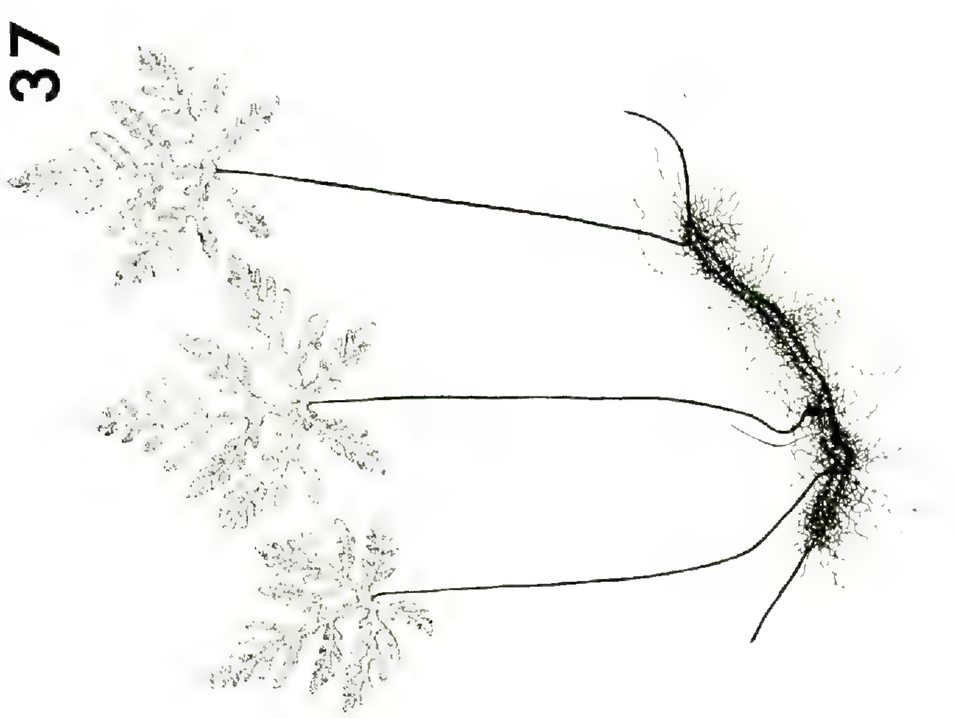
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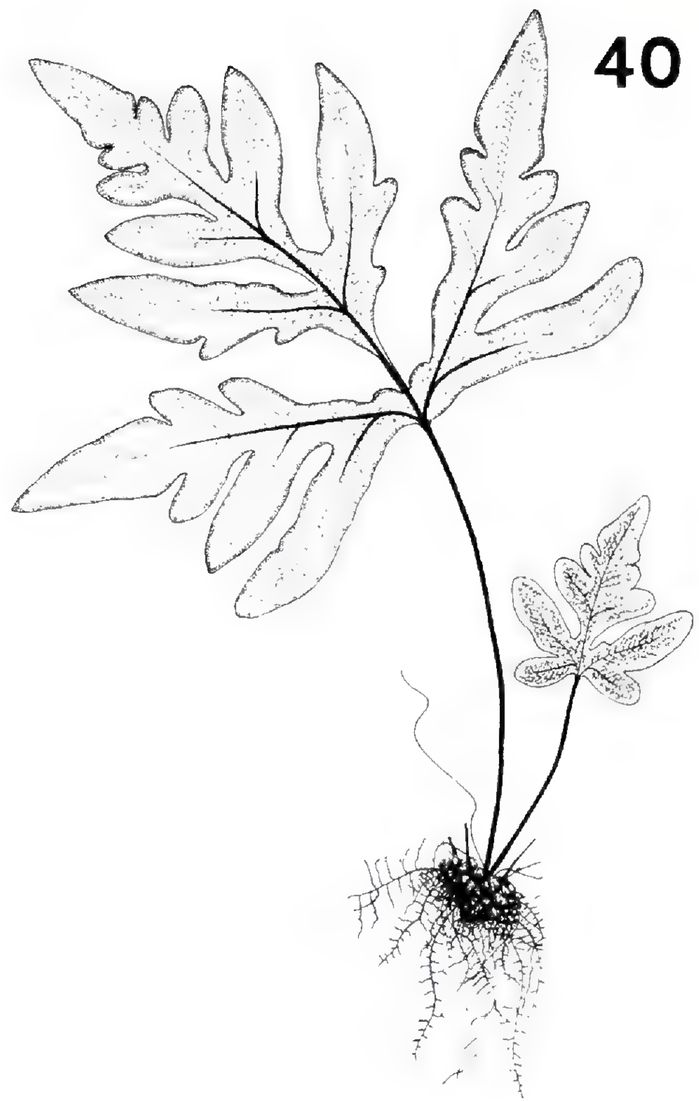

FIGURES 37–40. Line drawings of **Bommeria** species: 37, *B. hispida* (*Reeder, Reeder, & Soderstrom 3476*, YU), × ½; 38, *B. pedata* (*Pringle 1861*, UC), × ⅓; 39, *B. subpaleacea* (*Sanchez M. 195*, US), × ½; 40, *B. ehrenbergiana* (*Gastony & Haufler 1086*, IND), × ⅓.

forms" (i.e., one with areoles and a second with free veins) were collected together. In his published account (1883) he stated that specimens having open and areolate venation were "from the same lot" and so should be conspecific. *Gymnogramma hispida* was again separated from *G. ehrenbergiana* by Underwood (1902), since which time both have been consistently recognized as species.

In 1893 Pringle collected a dwarfed form of *Bommeria* (*Pringle 4420*) from xeric cliffs near Tequila, Jalisco, Mexico, and labeled his specimens as *Gymnogramma ehrenbergiana* (actually *B. hispida*) var. *muralis*. In a report of the plants collected by Pringle between 1891 and 1893, Davenport (1894) described this variety, attributing the name to Pringle. Davenport gave a brief diagnosis and cited Pringle's collection, but he did not indicate a holotype specimen. Accordingly, I have chosen the specimen annotated as being from the Davenport Herbarium as the holotype. In 1974 Gerald J. Gastony and I re-collected the putative variety from the same locality reported by Pringle and obtained living material for greenhouse culture. Under uniform greenhouse conditions it became clear that the putative dwarf variety was no more than an environmentally induced variant since the "dwarf" plants grew to be as large as some of the more typical *B. hispida* plants. Thus, the dwarf nature of this population is induced by the extremely xeric habitat in which it is found. Analysis of the morphology and chemistry of these plants indicated no significant characters to support varietal status for this colony.

A total of 343 collections of *Bommeria hispida* were examined during the course of this study. A geographically representative sample is given below.

REPRESENTATIVE SPECIMENS EXAMINED. **United States.** CALIFORNIA: without further locality, *Palmer s.n.* in 1876 (US); between San Diego and the Colorado, *Schott s.n.* (F). ARIZONA: without further locality, *Jones 4254* (CAS, DS, F, MICH, MSC, NY, UC, US); Arivaca, *Haufler & Haufler 4, 5* (GH, IND); Baboquivari Mts., *Gilman 18* (US), *Pringle s.n.* in 1884 (F, GH, NY, TEX, VT); Chiracahua National Forest, *Eggleston 10902* (US); Coronado National Forest, *Haufler & Haufler 6* (GH, IND); Dragoon Mts., *Vasey 1* (UC); Gardner Canyon, *Pinkava, Keil, & Lehto 16646* (ASU); Huachuca Mts., *Brown s.n.* (GH), *Darrow et al. 2543* (ARIZ, UC), *Gentry 3344* (UC), *Gooding 395* (UC); Pena Blanca Lake, *Keil et al. 9714a* (ASU), *Lemmon s.n.* in 1882 (CAS, DS, F, GH, MICH, MO, NO, NY, SD, UC, US, YU); Prescott, *Eastwood 16698* (UC, US), *Palmer 556* (NY, SD, UC, YU); Santa Rita Mts., *Cook s.n.* (US); *Griffiths 6055* (US), *Phillips 2318* (UC); Texas Canyon, *Lehto 2143* (ASU). NEW MEXICO: Cave Canyon, *Rusby 596* (CAS, GH, MO, NO, NY, UC, US, VT, YU); Gila National Forest, *Haufler & Haufler 7* (GH, IND); Guadalupe Canyon, *Mearns 695* (US); Hillsboro, *Greene s.n.* in 1880 (F); Organ Mts., *Finsley 1951* (F), *Wooton s.n.* in 1899 (DS, NY, UC); San Lorenzo, *Metcalfe 1477* (F, GH, UC); Silver City, *Eastwood 8269* (CAS, US). TEXAS: Adobe Draw, *Haufler & Haufler 3* (GH, IND); Alpine, *Soxman 232* (TEX); Big Bend National Park, *Brenckle 51046* (US); Chisos Mts., *Rossbach 4887* (US); Davis Mts., *Palmer 31859* (MO, TEX, US); Franklin Mts., *Correll 15036* (MO); Hueco Mts., *Correll 13794* (MO, TEX, UC); Limpia Canyon, *Soxman 459* (MICH); Little Aguja Canyon, *Moore & Steyermark 3042* (MICH, US); Mt. Livermore,

Hinckley 225 (TEX). **Mexico.** BAJA CALIFORNIA: without further locality, *Carter, Alexander, & Kellogg 2035* (DS, GH, MEXU, US); Cerro de la Giganta, *Gentry 4273* (ARIZ, DS, GH, MO, US); La Champagna, *Gentry & Fox 11773* (US); Volcán las Tres Virgenes, *Moran & Reveal 20209* (SD). SONORA: Canyon de la Escabena, *Phillips 269* (MICH); Canyon del Agua, *Phillips 778* (GH, MICH); Río de Bavispe, *White 4049* (MICH, US); Sierra de las Papas, *Gentry 607* (DS, MICH). CHIHUAHUA: Chihuahua, *Pringle 465* (F, MEXU, MICH, NY, TEX, VT), *Weber & Charette 11632* (UC, VT); Cuahutémoc, *Correll & Johnston 21596* (TEX, US), *Gould 8961* (TEX); Hidalgo de Parral, *Gentry 8267* (GH, MICH, UC, US); Mojarachic, *Knobloch 37* (F), *1147* (MSC); Mt. Kilo, *Knobloch 2059* (MSC); Santa Eulalia Mts., *Knobloch 641* (MSC); Sierra de Santa Barbara, *Correll & Gentry 22806* (GH, TEX); Vieja Casas Grandes, *Tucker 2567* (ARIZ, CAS, DAV, DS, UC, USC). COAHUILA: Del Carmen Mts., *Wynd & Mueller 575* (ASU, DAV, GH, ILL, MICH, MO, NY, US); Sierra del Jardin, *Chiang, Wendt, & Johnston 9316* (TEX). DURANGO: Durango, *Anderson & Laskowski 3563* (MICH), *Palmer 556* (F, GH, MEXU, MO, NY, UC, US); Otinapa, *Palmer 358* (F, GH, MO, NY, UC, US); Sandia Station, *Pringle 10151* (F, GH, MEXU, MICH, MO, NY, UC, US, VT). ZACATECAS: without further locality, *Morley 648* (UC); Pico de Tevia, *Lloyd 217* (US); *Valparaiso, McVaugh 17756* (MICH). SAN LUIS POTOSÍ: without further locality, *Parry & Palmer 1006* (F, GH, MO, NY, US, YU); *Schaffner 928* (GH, YU). JALISCO: La Venta, *Lemmon & Lemmon 55* (GH); Paso de la Troje, *McVaugh 16753* (MICH); Tequila, *Gastony & Haufler 1073* (GH, IND, MEXU), *Pringle 4420* (F, GH, MEXU, MICH, TEX, UC, US, VT). AGUASCALIENTES: Calvillo, *McVaugh 18309* (MICH). HIDALGO: Ixmiquilpan, *Rose, Rose, & Painter 8932* (US). MÉXICO: Temascaltepec, *Hinton 1431* (GH). **Nicaragua.** ESTELÍ: without further locality, *L. Gómez P. 1055* (CR).

2. **Bommeria pedata** (Sw.) Fourn. Bull. Soc. Bot. France 27: 327. 1880. FIGURE 38: MAP 1.

Hemionitis pedata Sw. Synopsis Fil. **20:** 209. 1806. TYPE: perhaps collected by Don Luis Née in Mexico, sent by Cavanilles to Swartz, presumably now at s (*n.v.*).
Gymnogramma pedata (as *pedatum*) (Sw.) Kaulf. Enum. Fil. 69. 1824.
Neurogramma pedata (Sw.) Link, Fil. Sp. Horto Berol. 139. 1841.
Gymnopteris pedata (Sw.) C. Chr. Index Fil. 341. 1905.

Rhizome short and seldom branched, dictyostelic, leaves arising at ca. 0.1 cm. intervals. Petiole castaneous to atropurpureous, terete to often sulcate at apex, scales common at base, occasional at apex, trichomes sparse at apex, central portion glabrous. Lamina 3.5–13.5 cm. in length; ultimate segments acute at apex; adaxial indument of unicellular, acicular trichomes (0.28–0.44 mm. in length) each arising from a rosette of specialized basal cells, abaxial indument of scales (with 2 to 8 cells across the base) and unicellular, acicular trichomes (0.38–0.84 mm. in length); rachis castaneous; venation open. Sporangia usually covering $\frac{2}{3}$–$\frac{3}{4}$ of the distance from the margin to the costa of each ultimate segment, occasionally marginally restricted. Spores 32 per sporangium; perispore surface reticulate.

DISTRIBUTION. Western and central Mexico through Guatemala, Honduras, Nicaragua, and into Costa Rica. Isolated plants arising from crevices

in cliffs and from under large boulders on rocky hillsides in mesic and xeric mountainous regions at altitudes of 900–2400 meters.

This species is the only one for which type material has not been seen, but the illustration of Swartz (1806) appears to be characteristic of plants assigned to the species.

Excluding the disjunct Nicaraguan population of *Bommeria hispida*, *B. pedata* has the greatest range of all *Bommeria* species. In all probability, the single most important factor contributing to this extensive distribution is the abbreviated life cycle of this apomictic triploid (see Tryon, 1968; Whittier, 1970).

A total of 125 collections of *Bommeria pedata* were examined during the course of this study. A geographically representative sample is given below.

REPRESENTATIVE SPECIMENS EXAMINED. **Mexico.** BAJA CALIFORNIA: El Taste, *Brandegee s.n.* in 1893 (NY, UC, YU). SONORA: Curahui, *Pennell 19673* (MEXU, US). CHIHUAHUA: Bahuichivo, *Bye 1662* (GH); Ceracahui, *Knobloch 916* (GH, MSC, US); Cuiteco, *Knobloch 856* (MSC); Urique, *Bye 1758* (GH). SINALOA: without further locality, *Knobloch 2142* (GH); El Quintero, *Breedlove & Thorne 18051* (NY). DURANGO: without further locality, *Garcia 796* (US). NAYARIT: Ahuacatatlán, *Feddema 387* (MICH), *McVaugh 16424* (MEXU, MICH, NY, US); Santa María del Oro, *Feddema 790* (MICH); Tepic, *Mexia 529* (GH, MEXU). ZACATECAS: Valparaiso, *McVaugh 17652* (MICH). JALISCO: Atequizallán, *Correll 14370* (F, TEX, US); Autlán, *Wilbur & Wilbur 2262* (MICH); Barranca de Oblatos, *Barnes & Land 125* (F); Chapala, *Rose & Painter 7666* (US); Ciudad Guzmán, *Cutler 4077* (G, US); Guadalajara, *Barkley, Paxson, & Rowell 7540* (TEX), *Pringle 1861* (F, GH, MO, NY, TEX, UC, US, VT); La Huerta, *Haufler & Brown 8* (GH, IND, MEXU); La Venta, *Lemmon & Lemmon 55* (F, GH, UC, US); Mazamitla, *McVaugh 12991* (MICH, US); Río Blanco, *Palmer 151* (MEXU, MO, NY, US, YU); Tapalpa, *Iltis & Koeppen 788* (GH, ILL, MICH, NY). VERA CRUZ: Cordoba, *Spence 109* (GH); Mt. Orizaba, *Bourgeau 2772* (UC), *Seaton 41* (F, GH, US). MICHOACÁN: Cerro Santa María, *Feddema 109* (MICH); Coalcomán, *Hinton 12210* (GH, MO, NY, TEX, US); Comanja, *Haufler & Brown 10* (GH, IND, MEXU); Cotija, *Haufler & Brown 9* (GH, IND, MEXU); Morelia, *Arsène 9934* (US); Quiroga, *Barkley & Burford 2719* (F); Uruapan, *Leavenworth & Hoogstraal 1235* (MO). MÉXICO: Luvianos, *Roe et al. s.n.* in 1965 (MICH); Nueva Ixtapan, *Mickel & Clewell 717* (MICH, NY); Río Hondo, *Rzedowski 29601* (CAS); Temascaltepec, *Hinton 1431* (GH); Tlalpam, *Fisher 4* (F, MO, US); Valle de México, *Schaffner 7* (MEXU, NY); Valle de Bravo, *Matuda 27186* (MEXU, US); Xochimilco, *Orcutt 4331* (US). MORELOS: Ahuacatitlán, *Sanchez M. 194* (US); Cuautla, *Boyd 33* (MICH); Cuernevaca, *Manning & Manning 53968* (GH, MEXU), *Rose & Painter 6921* (GH, US); El Parque, *Orcutt 4390* (MO, US); Huitzilac, *Lyonnet 754* (DS, GH, MO, NY, US); Teposteco, *Lyonnet 2576* (US); Xochicalo, *Kenoyer s.n.* in 1938 (ARIZ). PUEBLA: Tepoxuchil, *Nicolas s.n.* in 1909 (GH). GUERRERO: Chilpancingo, *Storer 109* (MICH); Manchon, *Hinton 9209* (ARIZ, GH, MO, NY, TEX, US); Taxco, *Clark 7240* (MO), *Haufler & Brown 11* (GH, IND, MEXU). OAXACA: Cerro de San Filipe, *Conzatti & Gonzalez 454* (GH, MEXU); Ixtlán, *Mickel & Clewell 806* (MICH); Río San Filipe, *Iltis, Iltis, & Koeppen 1209* (GH, MICH, NY); Sola de Vega, *Mickel 1659* (MICH); Sta. María Albarrados, *Mickel 824* (US). CHIAPAS: Amatenango, *Alava 1380* (MEXU, MICH); San Cris-

tóbal, *Münch 161* (DS). **Guatemala.** HUEHUETENANGO: Huehuetenango, *Steyermark 50411* (F, US). BAJA VERAPAZ: Santa Rosa, *Von Türkheim 112327* (NY, US). GUAJINIQUILAPA: without further locality, *Lehmann 1684* (US). GUATEMALA: without further locality, *Tonduz 688* (F, GH, MO, NY, US). JALAPA: Jalapa, *Standley 76724* (US). SUCHITEPÉQUEZ: Antiqua, *Standley 58633* (F). SANTA ROSA: Jumaytepeque, *Smith 4086* (GH, NY). SOLOLÁ: Pueblo San Jorge, *Hatch & Wilson 297* (GH, US); Volcán Santa Clara, *Steyermark 47299* (F, US). **Honduras.** MORAZÁN: *Molina R. 340* (US). **Nicaragua.** ESTELÍ: *L. Gómez P. 616* (CR). JINOTEGA: *Howard s.n.* in 1953 (US). **El Salvador.** LIBERTAD: *Thompson 53* (MO). **Costa Rica.** ALAJUELA: Volcán Tenario, *L. Gómez P. 69867* (CR).

3. **Bommeria subpaleacea** Maxon, Contr. U. S. Natl. Herb. **17**: 169. 1913. TYPE: Mexico, Puebla, August, 1909, *Purpus 4025* (holotype, US 841463!; isotypes, F!, GH!, MO!, UC!). FIGURE 39; MAP 3.

Bommeria knoblochii Maxon, Am. Fern Jour. **32**: 59. 1942. TYPE: Mexico, Chihuahua, Mojarachic, September 20, 1939, *Knobloch 6044* (holotype, US 1791245!; isotypes, DS!, GH!, MSC!).

Rhizome short and seldom branched, dictyostelic, leaves arising at ca. 0.1 cm. intervals. Petiole castaneous to atropurpureous, terete to often sulcate at apex, central portion largely glabrous. Lamina 2.0–11.0 cm. in length; ultimate segments acute to rounded at apex; adaxial indument of unicellular, acicular trichomes (0.21–0.58 mm. in length), each arising from a rosette of specialized basal cells, abaxial indument of scales (commonly with 10 or more cells across the base) and unicellular, acicular trichomes (0.38–0.98 mm. in length); rachis castaneous; venation areolate. Sporangia covering $\frac{2}{3}$–$\frac{3}{4}$ of the distance from the margin to the costa of each ultimate segment. Spores 64 per sporangium; perispore cristate.

DISTRIBUTION. Very restricted in the mountainous region of Chihuahua, Mexico, and slightly more extensive in Guanajuato, Hidalgo, México, Puebla, Oaxaca, and San Luis Potosí, Mexico. Under the edges of boulders and in rock crevices of cliffs in the mesic canyons of mountainous regions at altitudes of 1000–2000 meters.

In 1942, based on the Chihuahuan collections of I. W. Knobloch, Maxon described a new species of *Bommeria* and named the species for its collector. The only definitive character that Maxon used to distinguish *B. knoblochii* from *B. subpaleacea* was variance in the extent of leaf vein areolation. *Bommeria knoblochii* was said to be partially areolate, the areoles being confined to the portion of the lamina adjacent to the major veins. In contrast, *B. subpaleacea* was described as wholly areolate. Detailed examination of venation patterns demonstrates that this character is not useful in species delimitation (cf. FIGURES 9, 10). All other morphological and chemical characters indicate that the populations previously referred to *B. knoblochii* are conspecific with *B. subpaleacea*; as a result, the former name has been reduced to synonymy.

SPECIMENS EXAMINED. **Mexico.** CHIHUAHUA: Areponapuchic, *Knobloch 1368* (MSC); La Bufa, *Bye 6087* (GH), *Haufler 25, 28* (GH, IND, MEXU), *Knobloch 442* (MSC), *575* (MSC, US); Mojarachic, *Knobloch 8000* (MSC); Segorichi, *Knobloch 151* (MSC, US). GUANAJUATO: Xichú, *Kenoyer 2381* (GH). SAN LUIS POTOSÍ: without further locality, *Parry & Palmer 1006* (NY, YU). HIDALGO: Atotonilco, *Haufler & Brown 14* (GH, IND, MEXU); Barranca de Metztitlán, *Moore & Wood 4231* (GH); Huasca, *Sanchez M. 195* (US). MÉXICO: Valle de México, *Schaffner 7* (NY). OAXACA: Huajuapan, *Mickel & Leonard 4556* (NY).

4. **Bommeria ehrenbergiana** (Kl.) Underw. in Baillon, Dict. Bot. 448. 1876. FIGURE 40; MAP 4.

Gymnogramma ehrenbergiana Kl. Linnaea **20:** 411. 1847. TYPE: ad thermas prope grande in regno Mexico, *Ehrenberg 662* (holotype presumably at B, *n.v.*; isotype, UC 416920!).

Stegnogramme ehrenbergiana (Kl.) Fourn. Mex. Pl. **1:** 71. 1872.

Gymnogramma ehrenbergiana (Kl.) D. C. Eaton in S. Watson, Proc. Am. Acad. **18:** 184. 1883.

Gymnogramma podophylla Hooker, Sp. Fil. **5:** 152. 1864. TYPE: between Vera Cruz and Orizaba, Mexico, *Müller 719* (holotype, K, *n.v.*; isotype, NY fragment!).

Hemionitis podophylla (Hooker) J. Smith, Hist. Fil. 150. 1875.

Bommeria podophylla (Hooker) Fourn. Bull. Soc. Bot. France **27:** 328. 1880.

Rhizome short and seldom branched, dictyostelic, leaves arising at ca. 0.1 cm. intervals. Petiole atropurpureous, terete to commonly sulcate near apex, scales common at base, few at apex, central portion glabrous. Lamina 5.0–16.0 cm. in length; ultimate segments rounded at apex; adaxial indument of unicellular, acicular trichomes (0.25–0.49 mm. in length), each arising from a rosette of specialized basal cells, abaxial indument of scales (2 to 8 cells across the base) and unicellular, acicular trichomes (0.38–0.84 mm. in length); rachis atropurpureous $\frac{1}{2}$–$\frac{2}{3}$ distance from base to apex; venation areolate. Sporangia covering $\frac{1}{4}$–$\frac{1}{2}$ of the distance from the margin to the costa of each ultimate segment. Spores 64 per sporangium; perispore surface reticulate.

DISTRIBUTION. Restricted to the Sierra Madre Oriental in the states of Hidalgo, México, Nuevo León, Puebla, San Luis Potosí, and Vera Cruz, Mexico. Isolated plants in periodically moist woods along the sides of canyons in mountainous regions at altitudes of 1300–2200 meters.

SPECIMENS EXAMINED. **Mexico.** NUEVO LEÓN: Alamar, *Mueller & Mueller 662* (F, GH, MEXU, MICH). HIDALGO: Barranca de Tolimán, *Moore & Wood 4382* (GH); Jacala, *Chase 7422* (F, ILL), *Edwards 715* (ARIZ, DS, MO, TEX, US), *Fisher 37111* (GH, MO, NY, US), *Gastony & Haufler 1086* (GH, IND, MEXU, MO), *Kenoyer 395* (F, MO). SAN LUIS POTOSÍ: without further locality, *Poust 98* (NY). VERA CRUZ: Mt. Orizaba, *Seaton 492* (F, GH, US). MÉXICO: Carcania de Ixtapan de la Sal, *Matuda 28799* (US). PUEBLA: Hacienda Batán, *Riba, Tryon, & Tryon 411* (GH, MEXU); Hueyotlipan, *Arsène 2147* (MICH, UC); Tepoxuchil, *Nicolas s.n.* in 1909 (F, NY); Pont de México, *Arsène s.n.* in 1907 (F, GH, US), *7* (F, MEXU, UC, US), *1684* (MEXU).

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GENERIC RELATIONSHIPS IN THE ANDROMEDEAE (ERICACEAE)

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THIS INVESTIGATION of generic relationships within the Andromedeae DC. was undertaken in connection with a monograph of *Lyonia* Nutt. (Judd, 1978), a genus that has often been confused with several related genera (especially *Pieris* D. Don) and that has been divided by some botanists into several smaller genera. The results of the phenetic and phylogenetic studies presented below have reaffirmed the generic distinctiveness of *Lyonia* and have clarified relationships among the related genera *Pieris*, *Arcterica* Coville, *Craibiodendron* W. W. Smith, *Agarista* D. Don, *Agauria* Hooker f., and *Leucothoë* D. Don.

The tribe Andromedeae (Ericaceae subfam. Vaccinioideae, see Stevens, 1970, 1971; Watson, 1965; Watson *et al.*, 1967) as circumscribed by Stevens (1970, 1971) comprises *Andromeda* L., *Oxydendrum* DC., *Chamaedaphne* Moench, *Craibiodendron* (including *Nuihonia* Dop), *Lyonia*, *Pieris*, *Arcterica*, *Agauria*, *Agarista*, *Zenobia* D. Don, *Leucothoë*, *Gaultheria* L. (including *Chiogenes* Salisb. and *Pernettya* Gaudich.), *Pernettyopsis* King & Gamble, *Tepuia* Camp, and *Diplycosia* Blume. Of these, *Andromeda*, *Oxydendrum*, and *Chamaedaphne* are considered to be isolated genera (see Stevens, 1970), while the remaining taxa fall into two general groups that are referred to by Stevens (1970) and here as the *Lyonia* group and the *Gaultheria* group.

The *Lyonia* group of genera tends to have biseriate-stalked multicellular hairs; paired bracteoles that are often at or near the base of the pedicel; slender, geniculate filaments; and short, rather broad anthers with an area of white disintegration tissue at the anther-filament junction. Staminal appendages, when present, are spurs, and the style is often swollen. The cells of the seed coat are usually much elongated with rather thin walls, the foliar stomata are anomocytic, and the leaf epidermis is often lignified. Bands of fibers are found in the secondary phloem of all genera, and the chromosome numbers, where known, are all $x = 12$. Stevens (1970) included *Lyonia*, *Craibiodendron*, *Pieris*, *Arcterica*, *Agauria*, and *Agarista* in this group. In contrast, the *Gaultheria* group, which includes *Leucothoë*, *Zenobia*, *Gaultheria*, *Pernettyopsis*, *Diplycosia*, and *Tepuia*, has multiseriate-stalked multicellular hairs, bracteoles that are usually paired and are often borne at the top of the pedicel, and filaments that are often stouter and never geniculate. In *Gaultheria*, *Leucothoë*, and *Zenobia* the anthers have awns and disintegration tissue; in the remaining genera, these characters are lacking, and the anther thecae are prolonged into terminal tubules. The cells of the seed coat are variable in shape and thickness, the foliar stomata are often paracytic or nearly so, and the leaf epidermis is not lignified. The type and arrangement of lignified cells

in the phloem is variable, but these cells do not occur in bands. Chromosome numbers, where known, are $x = 11$, 12, and 13 (see Stevens, 1970). There are, however, many exceptions to the characters given above (see TABLE 1), and these groups (as pointed out by Stevens himself) are not so sharply defined. Most of the exceptions, which involve either *Agauria* and *Agarista* or *Pieris*, are discussed in more detail below.

Because *Lyonia* has often been fragmented into several genera (Small,

TABLE 1. Variation in selected morphological, anatomical, and cytological characters in Lyonia, Pieris, Arcterica, Craibiodendron, Agarista, Agauria, and Leucothoë.

CHARACTER	LYONIA SECT. ARSENOCOCCUS	LYONIA SECT. MARIA	LYONIA SECT. PIERIDOPSIS	LYONIA SECT. LYONIA	PIERIS SECT. PIERIS	PIERIS SECT. PHILLYREOIDES	PIERIS NANA (ARCTERICA)	CRAIBIODENDRON	AGARISTA	AGAURIA	LEUCOTHOË
PROSTRATE SHRUBS	-	-	-(+)	-	-	-	+	-	-	-	-
BANDS OF FIBERS IN PHLOEM (TWIGS)	+	+	+	+	+	+	+	+	+	+	-
PITH TYPE (H = HETEROGENEOUS, E = HOMOGENEOUS, C = CALLUNA)	H	E	E	E	H	H(E)	E	E	C	CA.H	VAR.
PLANT EVERGREEN	-	-/+	-(+)	+	+	+	+	+	+	+	+/-
BUD SCALES	2	2-6(-8)	2	2	3-6	(2)3-4	≥3	2(-4)	2-4(-6)	>2	>2
SUPERPOSED BUDS	-	-	-	-	-	-	-	+	-	-	-
ELONGATED ATTACHMENT OF BUD TO TWIG	-	-	-	-	-	+/-	-	+	-	-	+/-
ARRANGEMENT OF LEAVES (A = ALTERNATE, PV = PSEUDOVERTICILLATE, W = WHORLED)	A	A	A	A	A/PV	A/PV	W	A	A	A	A
NODE OFTEN 3 TRACES FROM 1 GAP	-	-	-	-	-	-	-	+	-	-	-
LEAVES REVOLUTE IN BUD	-	-	-	-	-	-	-	-	-/+	+	-
LEAVES LESS THAN 1.5 CM. LONG	-	-	-	-(+)	-	-	+	-	-(+)	-	-
LEAVES SERR-(UL)ATE	+	-	-	+/-	+	+	-	-	-(+)	-	+
DENSE LEAF VEIN RETICULUM	-	-	-	-	-	-	-	-	+	+	-
INTRAMARGINAL LEAF VEIN	-	-/+	-	-	-	-	-	-	-	-	-
FREE LEAF FIBERS	-	-	-	-	-	-(+)	-	+	-	-	-
LEAF EPIDERMAL CELLS DIVIDED	-	-	-	-	-	-	-	-	+	-	-
LEAF HYPODERMIS	-	-	-(+)	+(-)	-	-	-	+/-	-	+	-
LEAF EPIDERMIS LIGNIFIED	-(+)	-(+)	-(+)	+	-/+	-/+	+	+	+	+	-
LEAF MIDRIB BUNDLE BIFACIAL	+	+(-)	+	+	-	-(+)	-	+	-	-	-

TABLE 1. CONTINUED

CHARACTER	Lyonia sect. Arsenococcus	Lyonia sect. Maria	Lyonia sect. Pieridopsis	Lyonia sect. Lyonia	Pieris sect. Pieris	Pieris sect. Phillyreoides	Pieris nana (Arcterica)	Craibiodendron	Agarista	Agauria	Leucothoë
Stomata anomocytic	+	+	+	+	+	+	+	+	+	+	-
Abaxial leaf epidermis papillose	-	-	-/+	-	-	-	-	-	-	+	-
Abaxial leaf surface densely covered with unicellular hairs	-	-	-	-/+	-	-	-	-	-(+)	-	-
Long-celled hairs	-	-	-	-	-/+	-	-	-	-	-	-/+
Multiseriate stalked-glandular hairs	-	-	-	-	-	-	-	-	+	+	+
Peltate scales	-	-	-	+	-	-	-	-	-	-	-
Multicellular swollen-headed hairs	+	+	+	+	-	-	-	-	-	-	-
Inflorescence position (A = axillary, T = terminal)	A	A	A	A	A/T	A	A	A	A	A	A
Inflorescence type ('P' = paniculate: raceme of fascicles, F = fascicle, R = raceme, 'R' = raceme with flowers in whorls of 3, P = panicle)	'P'	F	R	F(R)	P(R)	R	'R'	P	R	R	R
Inflorescence exposed in winter	-	-	-	-	+	+	+	-	-	-	+
Bracteole position (B = base, A = apex)	B	B	B	CA.B	LO.1/4 UP.1/4	LO.1/4 A	UP. 1/3	LO. 1/3	LO. 1/3	LO. 1/3	B TO A
Relationship of bracteoles (A = alt., O = opp.)	O	O	O	O(A)	A(O)	A(O)	A	A/O	A/O	A/O	A/O
Flower articulate with pedicel	+	+	+	+(-)	+	+	+	+	+	+	+
Aestivation of calyx lobes (V = valvate, I = imbricate)	V	V (OPENING EARLY)	V	I	V	V (OPENING LATE)	V	I	I	I	I
Prominent sepal fibers	-	-	-	-	+	+	+	-	-	-	-
Adaxial calyx stomata	-	-	-	-	+	+(-)	-	-	-	-	-

TABLE 1. CONTINUED

CHARACTER	*Lyonia* sect. *Arsenococcus*	*Lyonia* sect. *Maria*	*Lyonia* sect. *Pieridopsis*	*Lyonia* sect. *Lyonia*	*Pieris* sect. *Pieris*	*Pieris* sect. *Phillyreoides*	*Pieris nana* (*Arcterica*)	*Craibiodendron*	*Agarista*	*Agauria*	*Leucothoë*
Merosity (corolla)	5	5	5	4-7(8)	5	5	5	5	5	5	5
Corolla campanulate	-	-	-	-(+)	-	-	-	+	-	-	-
Corolla fleshy	-	-	-	-(+)	-	-	-	+	-	-	-(+)
Abaxial corolla stomata	+	+	+	+	-	-	-	+	+	+	+
Filaments geniculate	+	+	+	+	-	-(+)	-	+	+	+	-
Stamens with spurs	+	+	+/-	+/-	+	+	+	-	-	-	-
Location of spurs (F = filament, J = anther-filament junction)	F	F	F	F	J	J	J	NA	NA	NA	NA
Disintegration tissue on spurs	+	+	+	+	-	-	-	NA	NA	NA	NA
Pubescence of filaments (H = unicellular hairs, P = papillae or small projections, S = smooth)	H	H/P	H(P)	P	H	H(S)	P	P	H	H	H/P/S
Anthers with awns	-	-	-	-	-	-	-	-	-	-	+(-)
Capsule with thickened sutures	+	+	+(-)	+	-	-	-	-	-	-	-
Placenta position (on columella of capsule: SA = subapical, C = central, B = basal, A = apical)	SA	C(±B)	SA(C)	SA	SA	C/±B	±B	SA	A(C)	B	A
Seed coat cells (S = short, L = long)	L	L	L	L	L	S	L	L	L	L	S
Seeds winged (SL = slightly)	-	-	-	-	-/2SL	-	-(SL)	1	-	-	- OR BULGING CELLS
Chromosome no. (N =)	12	12	12	12	12	?	?	?	12	?	11
Geography (N = North America, W = West Indies, E = Eastern Asia, N A = Africa, S = South America)	N W	E	W N	E N	N W E	E	E	S N	A	N E
Number of species	1	2	5	27	3	3	1	4?	34?	1	8

Note: rare or uncommon character states are given in parentheses.

1914, 1933; Britton & Brown, 1913) and confused with *Pieris* (Gray, 1878; Bentham & Hooker, 1876; De Candolle, 1839; D. Don, 1834; G. Don, 1834), I have attempted to reassess the generic limits within the *Lyonia* group. *Leucothoë* has also been included in this study for two reasons. First, *Agarista* has often been treated as a section of *Leucothoë* (De Candolle, 1839; Sleumer, 1959). Second, several species of *Pieris* and *Lyonia* have been considered by earlier botanists (De Candolle, 1839; Richard in Sagra, 1850) to be species of *Leucothoë*, and Lems found in a study of leaf anatomy in the Andromedeae (1964) that *Lyonia lucida* (here placed in *Lyonia* sect. MARIA) was quite similar to *Leucothoë axillaris* and *L. fontanesiana*.

PHENETIC STUDY

In the present study the six genera of the *Lyonia* group, along with *Leucothoë*, were compared on the basis of 50 morphological, anatomical, and cytological characters (TABLE 1). Each genus was considered to be an "Operational Taxonomic Unit" (OTU), except *Lyonia* and *Pieris*, which are quite variable and in which each section was treated as an independent OTU. To produce a matrix of character differences (TABLE 2), each OTU was compared with every other, and the number of characters for which each pair of taxa exhibits different states was recorded. When two or more states of a given character are common within a single OTU, then that OTU, when compared to a second OTU, was scored as similar in that character even if only one of the character states matched the character state(s) possessed by the second OTU. However, character states that were rare or uncommon within an OTU were not taken into consideration in the numerical analysis, although they are shown within parentheses in TABLE 1. A phenogram (FIGURE 1) was then constructed (using the matrix of character differences presented in TABLE 2) by calculating the character differences between the OTUs (or OTU clusters) and successively joining the most similar OTUs.

It is evident from this purely phenetic approach that one can recognize five groups of morphologically and anatomically similar OTUs among the taxa considered (see TABLE 2 and FIGURE 1). The OTUs within each group (above steplike line in TABLE 2) differ from each other by 3 to 8 (to 11) characters, while any two OTUs from different groups, when compared, differ in (12 to) 14 to 22 characters (below steplike line in TABLE 2). These groups correspond to (1) *Arcterica* and *Pieris*, (2) *Lyonia*, (3) *Craibiodendron*, (4) *Agarista* and *Agauria*, and (5) *Leucothoë* (see also FIGURE 1). The joining of *Arcterica* with *Pieris* (at 10.5 character differences) is in the "gray area" between OTUs that are clearly very closely related (differing in only a few characters) and those that are quite distinctive (differing in 14 or more characters). Thus, the separation of the *Arcterica-Pieris* group into two phenetic groups would also be consistent with the information presented in FIGURE 1 and TABLE 2. However,

TABLE 2. Matrix of character differences.

	ARCT	PIER	PHIL	PIED	ARSE	MARI	LYON	CRAI	AGAR	AGAU	LEUC
ARCT	—										
PIER	10	—									
PHIL	11	4	—								
PIED	19	18	17	—							
ARSE	21	16	16	3	—						
MARI	17	16	16	3	4	—					
LYON	19	20	20	7	8	6	—				
CRAI	21	22	22	17	19	16	14	—			
AGAR	19	16	16	14	16	14	15	14	—		
AGAU	20	18	16	16	18	16	16	16	5	—	
LEUC	19	13	13	18	18	18	20	19	12	15	—

ARCT = *Pieris nana* (*Arcterica*); PIER = *Pieris* sect. PIERIS; PHIL = *Pieris* sect. PHILLYREOIDES; PIED = *Lyonia* sect. PIERIDOPSIS; ARSE = *Lyonia* sect. ARSENOCOCCUS; MARI = *Lyonia* sect. MARIA; LYON = *Lyonia* sect. LYONIA; CRAI = *Craibiodendron*; AGAR = *Agarista*; AGAU = *Agauria*; LEUC = *Leucothoë*.

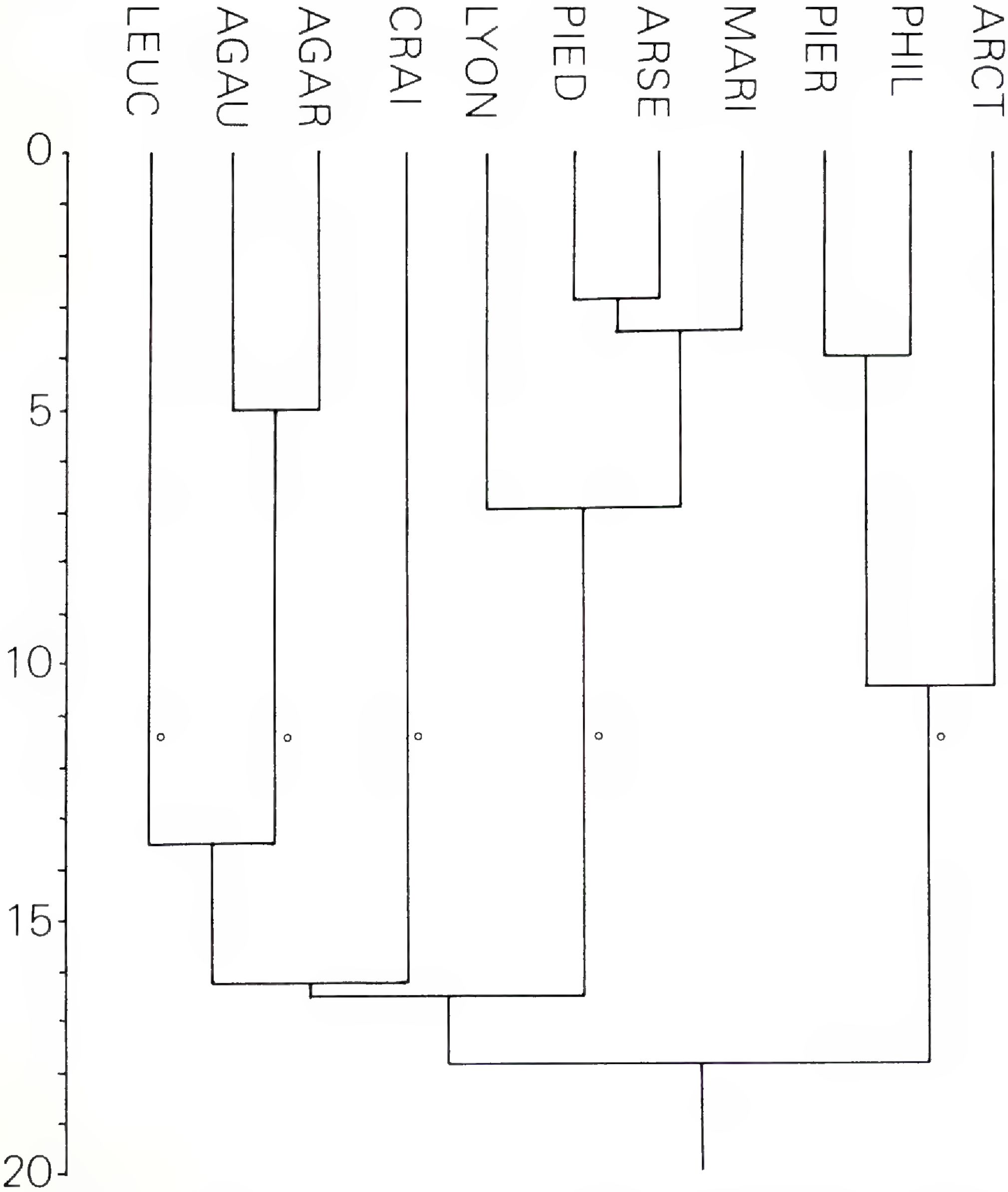

FIGURE 1. Phenogram based on character differences given in TABLE 2. ARCT = *Pieris nana* (*Arcterica*); PHIL = *Pieris* sect. PHILLYREOIDES; PIER = *Pieris* sect. PIERIS; MARI = *Lyonia* sect. MARIA; ARSE = *Lyonia* sect. ARSENOCOCCUS; PIED = *Lyonia* sect. PIERIDOPSIS; LYON = *Lyonia* sect. LYONIA; CRAI = *Craibiodendron*; AGAR = *Agarista*; AGAU = *Agauria*; LEUC = *Leucothoë*. An open circle (°) indicates each of the five phenetic groups discussed in the text.

because of the nature of the characters differentiating these two OTUs (see discussion below), they have been considered together.

Arcterica and *Pieris* are characterized by buds with 3 to 6 imbricate scales; leaves often pseudoverticillate; vascular bundle of the petiole or leaf midrib usually unifacial; fully mature flower buds that "overwinter" (i.e., inflorescences exposed for some time before flowering and with mei-

osis occurring in autumn); bracteoles variable in position but not at the base of the pedicel; calyx lobes stout, valvate in bud, and with prominent fiber strands associated with the vascular bundles (see Palser, 1951; Stevens, 1969); corollas lacking stomata on their abaxial surfaces; and filaments usually straight, with a pair of stout spurs at the anther-filament junction. In *Pieris* and *Arcterica*, the disintegration tissue does not extend onto the spurs. The monotypic *Arcterica* (*A. nana*) is phenetically much more similar to *Pieris* than to any other genus studied, differing only in having very small, entire-margined leaves that are in whorls of three, racemes in which the flowers are similarly whorled, twigs with a homogeneous pith, calyx lobes lacking stomata on their adaxial surfaces, and roughened-papillose filaments. It also differs in being a low, nearly prostrate, "heath-like" shrub. All of these characters except leaf arrangement vary infrageneric ally in one or more of the related genera. For example, the pith type is variable within *Lyonia*, *Pieris*, *Leucothoë*, and, to some extent, *Agauria*; stomata distribution on the calyx lobes differs in *Pieris*; and the filament indumentum varies within *Lyonia*, *Pieris*, and *Leucothoë*. From a phenetic standpoint it would appear that *Arcterica nana* does not possess sufficient morphological and anatomical distinctions to merit generic status; rather, it would be better treated as an isolated species within *Pieris* (perhaps in a section or subgenus by itself). Thus, in the remaining portion of the study, this species is referred to as *Pieris nana*. The relationships among the taxa included within *Pieris* will be discussed in more detail in a later paper.

Phenetically, *Lyonia* is a rather distinctive genus characterized by its buds with 2 scales (except in *L. mariana*), indumentum of biseriate-stalked multicellular hairs with more or less large, swollen heads, twigs usually with homogeneous pith, petiole or leaf midrib with a bifacial vascular bundle (except in *L. lucida*), inflorescences "overwintering" in the bud (i.e., not exposed for some time before flowering) with meiosis occurring in the spring, bracteoles usually opposite to subopposite and basal or nearly basal, calyx lobes lacking prominent fibers, and slender, geniculate filaments lacking appendages or having 2 spurs near the apex. In *Lyonia* the disintegration tissue of the anthers always extends onto the 2 rather slender spurs, when they are present, and in some taxa the filament spurs are actually completely disintegrated due to the development of this tissue. A final character unique to this genus is the distinctive thickened sutures of the capsule that in dehiscence often separate as a unit from the adjacent valves. (These distinctive sutures are present in all species except the rare eastern Asian *L. compta* and *L. chapaensis*.)

The recognition of any of the sections of *Lyonia* as genera is unwarranted because the number of distinguishing characters is relatively few. By comparison, there are many similarities between the sections; these distinguish *Lyonia* sensu lato from *Pieris*, *Craibiodendron*, *Leucothoë*, and other Andromedeae. Three genera — *Desmothamnus* Small, *Neopieris* Britton, and *Arsenococcus* Small — have been proposed as segregates from *Lyonia*.

Desmothamnus (Small, 1913, 1914, 1933), the only species of which is *D.* (*Lyonia*) *lucidus*, differs from the other species of *Lyonia* only in its leaves with an intramarginal vein, and in the unifacial vascular bundle of the petiole and leaf midrib. On various plants I have found occasional petioles that are slightly bifacial near the apex, and the venation type is quite variable among the remaining species of *Lyonia*, ranging from brochidodromous to eucamptodromous or nearly acrodromous (venation terminology *sensu* Hickey, 1973, and Dilcher, 1974). *Lyonia lucida* shares many characters with *L. mariana*, which was considered by Small (1914, 1933) to be the sole species comprising the genus *Neopieris*, although Britton and Brown (1913) had earlier placed both taxa in *Neopieris*. *Lyonia mariana* differs from other species of *Lyonia* only in its prominently urn-shaped capsules and deciduous calyx lobes, although the calyx lobes of *L. macrocalyx*, an eastern Asian species, are also occasionally deciduous. When considered together, *Lyonia mariana* and *L. lucida* differ consistently from other species of *Lyonia* only in their indumentum of multicellular, short-headed hairs and their buds with 2 to 6 (to 8) imbricate bud scales. To base genera on so few and such variable characters does not seem justifiable and certainly is not consistent with the magnitude of morphological discontinuities separating other commonly recognized genera in the Andromedeae.

Small (1913, 1914, 1933) treated *Lyonia ligustrina* as the genus *Arsenococcus*. (He included the morphologically distinctive populations of the Coastal Plain of the southeastern United States, which he considered to be *A. frondosa*, as a separate species.) Only its heterogeneous pith and paniculate inflorescences separate this taxon from the remaining species of *Lyonia*. Since the inflorescence type is variable within *Pieris* and, to some extent, in *Agarista*, since the pith type varies infragenerically in *Leucothoë*, *Pieris*, and slightly in *Agauria*, and since *Lyonia ligustrina* shows nearly all of the anatomical and morphological peculiarities of *Lyonia* listed above, it would be illogical to exclude this taxon. The Asian species (i.e., *Lyonia* sect. PIERIDOPSIS) are rather similar to *L. ligustrina* and help to ally this taxon even more closely with the remainder of the genus.

Although *Lyonia* sect. PIERIDOPSIS has often been referred to *Pieris*, this group differs from *Pieris* in its 2 large, imbricate bud scales; entire-margined and often deciduous leaves, which are not pseudoverticillate; indumentum of multicellular hairs with large, swollen heads; homogeneous pith; bifacial vascular bundle of the petiole; exclusively axillary and racemose inflorescences; opposite and basal bracteoles; lack of adaxial calyx stomata; presence of abaxial corolla stomata; geniculate filaments; spurs (when present) arising from the filament and with disintegration tissue; capsules with thickened sutures; calyx lobes lacking prominent fiber strands; and inflorescence "overwintering" within the bud. Species of *Lyonia* sect. PIERIDOPSIS were included in *Pieris* only because of the emphasis given to the presence of staminal spurs in *Lyonia ovalifolia*. It was thought that because this species (and several of its relatives) possessed this "key character" of *Pieris*, it must be placed in the genus (see

G. Don, 1834; De Candolle, 1839; Bentham & Hooker, 1876; Gray, 1878; J. D. Hooker, 1882; Brandis, 1911; Lecomte, 1930). In addition, some of the characters listed above were either unknown or misinterpreted by earlier botanists. The same reasoning was applied to *Lyonia lucida* and *L. mariana* (sect. MARIA), which have well-developed spurs near the apex of their filaments, and the result was the same (see Bentham & Hooker, 1876; Small, 1903). Actually, the spurs of *Lyonia ligustrina* (sect. ARSENOCOCCUS) are small, while those of several of the West Indian lyonias (sect. LYONIA) are quite well developed, but this fact was not known at the time. The spurs of *Lyonia* are, in reality, quite different from those of *Pieris*: in *Lyonia* they always arise from the filament and have a line of white disintegration tissue running along their upper margin; in *Pieris* they are at the anther-filament junction, and the disintegration tissue never extends onto the spurs. *Lyonia* sect. PIERIDOPSIS is best included in *Lyonia* because its taxa possess the complex of characters (given above) that characterize this genus. The section differs from the rest of the genus only in having racemose inflorescences.

Niedenzu (1890) considered *Lyonia* sect. LYONIA and *Chamaedaphne* to be congeneric, chiefly because they both have peltate scales. *Chamaedaphne* is in fact not very close to *Lyonia* sect. LYONIA, differing from it in its usually more or less paracytic stomata, apical bracteoles, stamens with straight filaments lacking appendages, anthers with terminal tubules, terminal inflorescences, unifacial leaf midrib bundle, capsules lacking thickened sutures, and presence of the yellow flavonol gossypetin (see Harborne & Williams, 1973). Even the leaf scales of the two groups are only superficially similar. The scales of *Lyonia* sect. LYONIA often have quite elongated stalks and fimbriate or irregular margins, while those of *Chamaedaphne* have very short stalks and nearly entire margins. The cells composing the scales of *Chamaedaphne* are also smaller and more regularly arranged.

Phenetically, *Craibiodendron* is an isolated genus characterized by its often superposed buds, which have 2 (to 4) bud scales and a rather elongated attachment to the twig; twigs with a homogeneous pith; bifacial vascular bundle of the petiole and leaf midrib; indumentum of biseriate-stalked, small-headed, multicellular hairs; axillary paniculate inflorescences with terminal flowers that "overwinter" within the bud; bracteoles usually positioned in the lower ⅓ of the pedicel; clearly imbricate calyx lobes; more or less campanulate and carnose corollas; roughened-papillose and geniculate filaments that lack appendages; and large, thick-walled capsules bearing a few large seeds, each with a prominent unilateral wing.

Agauria and *Agarista* are characterized by buds with more than 2 bud scales; an indumentum of multiseriate-stalked, small-headed, multicellular hairs; leaves with a unifacial midrib bundle and a rather dense vein reticulum with all orders more or less equally prominent; bracteoles usually positioned in the lower ⅓ of the pedicel; and geniculate filaments without appendages and covered with long unicellular hairs. In addition, the single species of *Agauria* and at least some species of *Agarista* have leaves that

are revolute in bud. The relationship between these two supposed genera and the characters by which they differ are discussed in detail by Stevens (1970), but it should be added that all the characters by which these two taxa differ (e.g., pith type, presence of papillae on abaxial leaf epidermis, placenta position, presence of a leaf hypodermis) are variable — infrageneically as well as infraspecifically — in at least one of the other major phenetic groups. *Agarista* and *Agauria* are phenetically very similar (TABLE 2 and FIGURE 1) and should be reunited into a single genus.

Leucothoë is distinguished by its indumentum of multiseriate-stalked hairs, unifacial leaf midrib bundle, leaves with an unlignified epidermis and paracytic stomata, lack of fiber bands in the phloem of the twigs, imbricate calyx lobes, "overwintering" of nearly mature flower buds (i.e., inflorescences exposed in winter), straight filaments, anthers with awns (in some species), seeds with testa cells not elongated, and chromosome numbers (where known) of $x = 11$. This genus is distinct from the other genera (including *Agarista* and *Agauria*) in its awns, paracytic stomata, chromosome number, and lack of fiber bands in the phloem. *Leucothoë* also differs from all taxa studied (except *Pieris cubensis*, *P. swinhoei*, and *P. phillyreifolia*) in having seeds with the testa cells not strongly elongated. *Leucothoë* seems to be most similar to *Agarista/Agauria* and *Pieris*, but the magnitudes of the differences between these genera are such that to include either within *Leucothoë* would completely destroy the distinctive character combinations shown by these genera. The similarities of *Leucothoë* (in the *Gaultheria* group) with *Pieris* and *Agarista/Agauria* (in the *Lyonia* group) are likely due to the retention of many common primitive characters in these genera (but a few cases of parallel evolution may also be involved; see cladistic study). The relationships of *Leucothoë*, *Agarista*, and *Agauria* are discussed in detail by Stevens (1970).

CLADISTIC STUDY

The phenetic approach to the problem of generic limits discussed above is useful in suggesting phenetic affinities between groups, but much phylogenetic or cladistic information is lost or distorted by this method (see Hennig, 1966; Kavanaugh, 1972; Bremer & Wanntorp, 1978). Therefore, I have attempted to determine the phylogenetic or cladistic relationships (i.e., similarities due to synapomorphies) between and among the genera of the *Lyonia* group and *Leucothoë*. Taxa are grouped by their shared derived characters (synapomorphies) in accordance with the application of the criterion of parsimony. As in all cladistic methods, a great problem is to determine for each character which state is derived and which is ancestral (see Mayr, 1965, 1969; Ehrendorfer, 1976; Funk & Stuessy, 1978; and Stuessy, 1979, for other difficulties and for discussions concerning the application of cladistic methods).

Forty-five characters were used and assigned generalized (primitive, ancestral, or plesiomorphous) or specialized (advanced, derived, or apomorphous) states using the method of Wagner (1961, 1962, 1969). TABLE 3 lists these characters. Each taxon or OTU was scored 0 if generalized

TABLE 3. Characters used in phylogenetic study (Wagner method) of the genera of the Lyonia group of the Andromedeae.

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
A	Habit	Trees to low shrubs	Prostrate, "heathlike"
B	Bands of fibers in the phloem	No	Yes
C	Pith	Homogeneous	a. Heterogeneous b. *Calluna*-type
D	Bud scales	2 small, opening to reveal several additional	a. Only 2 visible; large to small, imbricate b. 3, imbricate c. Many, small, imbricate, clearly spirally arranged
E	Number of buds/ leaf axil	1	2, superposed
F	Attachment of bud to stem	Short	Elongated
G	Arrangement of leaves	Alternate, ± equally spaced	a. ± pseudoverticillate b. In whorls of 3
H	Leaves deciduous	No	Yes
I	Vascular anatomy of node	1 trace from 1 gap	Often 3 traces from 1 gap
J	Arrangement of leaves in bud	Convolute	Revolute
K	Size of leaves	>1.5 cm.	<1.5 cm.
L	Leaf margin	Entire	Serrate or serrulate
M	Vein reticulum of leaf rather dense, all veins ± equally prominent	No	Yes
N	Fiber strands in leaf mesophyll	No	Yes
O	Epidermal cells of leaf divided	No	Yes
P	Adaxial leaf hypodermis present	No	Yes
Q	Leaf epidermis	Not lignified	Lignified

TABLE 3. Characters used in phylogenetic study (Wagner method) of the genera of the Lyonia group of the Andromedeae (*continued*).

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
R	Petiole and leaf midrib vascular bundle	Unifacial	Bifacial
S	Stomata	Anomocytic	Paracytic
T	Abaxial leaf epidermis papillose	No	Yes
U	Abaxial leaf epidermis densely covered with unicellular hairs	No	Yes
V	Structure of stalk of multicellular hairs	Multiseriate	Biseriate
W	Peltate scales	Lacking	Present
X	Structure of head of multicellular hairs	Small	Large, swollen
Y	Head of multicellular hairs elongated	No	Yes
Z	Inflorescence type	Panicles (with terminal flowers)	a. Panicles (lacking terminal flowers) b. Racemes (lacking terminal flowers) c. Fascicles (lacking terminal flowers) d. Panicles (terminal, lacking terminal flowers) e. Racemes with flowers in whorls of 3 (lacking terminal flowers)
AA	Inflorescence "over-wintering" within bud	Yes	No
BB	Bracteole position	Tending to be positioned in lower ⅓ of pedicel	a. Basal (or nearly so) b. Variable, near apex to within ca. lower ⅓ of pedicel

TABLE 3. Characters used in phylogenetic study (Wagner method) of the genera of the Lyonia group of the Andromedeae (*continued*).

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
CC	Aestivation of calyx	Imbricate	Valvate
DD	Prominent fiber strands present in calyx lobes	No	Yes
EE	Adaxial calyx stomata present	No	Yes
FF	Number of flower parts	Usually 5-merous	4-, 6-, or 7-merous
GG	Corolla shape	Urceolate to cylindrical	± campanulate
HH	Thickness of corolla	Thin	Thick
II	Abaxial corolla stomata present	Yes	No
JJ	Filament shape	± straight	Geniculate
KK	Spurs present	No	Yes (but in some taxa probably secondarily lost)
LL	Spurs with disintegration tissue	No	Yes
MM	Indumentum of filaments	Unicellular hairs	a. Papillae b. Smooth
NN	Anthers with awns	No	Yes
OO	Capsule sutures	Unthickened	Thickened
PP	Placenta position	Apical or ± subapical	Basal to ± central
QQ	Cells of seed coat	± isodiametric	Strongly elongated
RR	Wings present	No	a. Yes; a single large wing on one side of seed b. Yes; a fimbriate wing around seed formed by outgrowths of individual cells c. Yes; a narrow wing on each side of seed
SS	Chromosome number	$x = 12$	$x = 11, 13$, etc.

and 1 if specialized for each of the characters. When two or more states of a given character are considered derived, each is given a lower-case alphabetic superscript (e.g., 1^a, 1^b, 1^c). When both derived and generalized states of a character commonly occur within a single taxon, the abbreviation "var." for variable is recorded for this character. In the cladistic analysis this "var." condition is scored as a 1. If a character state occurs only rarely within an OTU, it is listed within parentheses after the predominating character state and is not considered in the cladistic analysis. (These two means of dealing with characters that vary within OTUs may introduce some slight distortion into the phylogenetic relationships determined.) All the taxa are listed in TABLE 4, with the character state values for each. The total divergence index of each taxon (or OTU) was determined by adding the individual character state values of each character. Then mutual groupings of derived characters between taxa were determined (by hand), and the taxa were arranged in sequence according to these groupings. They were plotted on a concentric graph (FIGURE 2), the branching points being determined by the mutual groupings of characters and the distance being determined by the divergence of each taxon. Thus, only the branching points and the evolutionary divergence values (i.e., the length of the lines) indicated by this figure are meaningful.

The Wagner method requires numerous assumptions concerning which is the derived and which is the generalized state of each character. Although these decisions were made after an extensive study of *Lyonia* and related genera, they are inevitably often rather subjective and thus introduce a major source of error.

Character states considered as derived for functional or ecological reasons include: leaves deciduous; habit low, heathlike, shrubby; adaxial calyx stomata present; "overwintering" of nearly mature flower buds; buds with two large, imbricate scales; anther filaments geniculate; staminal spurs present; sepals with prominent fiber strands; seeds variously winged; capsules with thickened sutures; and leaves less than ca. 1.5 cm. long. The role of function in the evolutionary interpretation of comparative data is considerable (see discussion in Simpson, 1961; Davis & Heywood, 1963; Mayr, 1969; Stebbins, 1974), especially when the functional/ecological analysis of homologous characters is carried out across several related taxonomic groups (i.e., out-group comparison). Functionally specialized characters found in one or a few taxonomic groups (and not in the out-groups) are considered derived.

Deciduous leaves occur in groups that are otherwise (e.g., in anatomy, floral morphology) very different, and it seems likely that they have evolved independently where this character is of adaptive value. For example, the deciduous *Lyonia ovalifolia* var. *elliptica* occurs in cool to warm-temperate areas of Japan, while the related semi-evergreen var. *rubrovenia* [1] is a plant of the warm and moist forests of Hainan. Both

[1] **Lyonia ovalifolia** (Wallich) Drude var. **rubrovenia** (Merrill) Judd, comb. nov. (*Pieris rubrovenia* Merrill, Philip. Jour. Sci. **23**: 256. 1923).

TABLE 4. **Character states used in the construction of the Wagner Tree.**

Character	*Lyonia* sect. *Arsenococcus*	*Lyonia* sect. *Pieridopsis*	*Lyonia* sect. *Maria*	*Lyonia* sect. *Lyonia*	*Pieris* sect. *Pieris*	*Pieris* sect. *Phillyreoides*	*Pieris nana* (*Arcterica*)	*Craibiodendron*	*Agarista*	*Agauria*	*Leucothoë*
A	0	0(1)	0	0	0	0	1	0	0	0	0
B	1	1	1	1	1	1	1	1	1	1	0
C	1a	0	0	0	1a	1a(0)	0	0	1b	1a	var.
D	1a	1a	var.(c)	1a	0	0	1b	1a	0	0	0
E	0	0	0	0	0	0	0	1	0	0	0
F	0	0	0	0	0	var.	0	1	0	0	var.
G	0	0	0	0	1a	1a	1b	0	0	0	0
H	1	1(0)	var.	0	0	0	0	0	0	0	var.
I	0	0	0	0	0	0	0	1	0	0	0
J	0	0	0	0	0	0	0	0	0(1)	1	0
K	0	0	0	0(1)	0	0	1	0	0	0	0
L	1	0	0	var.	1	1	0	0	0(1)	0	1
M	0	0	0	0	0	0	0	0	1	1	0
N	0	0	0	0	0	0(1)	0	1	0	0	0
O	0	0	0	0(1?)	0	0	0	0	1	0	0
P	0	0(1)	0	1(0)	0	0	0	var.	0(1)	1	0
Q	0(1)	0(1)	0(1)	1	var.	var.	1	1	1	1	0
R	1	1	1(0)	1	0	0(1)	0	1	0	0	0
S	0	0	0	0	0	0	0	0	0	0	1
T	0	var.	0	0	0	0	0	0	0	1	0
U	0	0	0	var.	0	0	0	0	0(1)	0	0
V	1	1	1	1	1	1	1	1	0	0	0
W	0	0	0	1	0	0	0	0	0	0	0
X	1	1	1	1	0	0	0	0	0	0	0
Y	1	1	0	0	0	0	0	0	0	0	0
Z	1a	1b	1c	1c	1d	1b	1e	0	1b	1b	1b
AA	0	0	0	0	1	1	1	0	0	0	1
BB	1a	1a	1a	1a(0)	1b	1b	1b	0	0	0	1b
CC	1	1	1	0	1	1	1	0	0	0	0
DD	0	0	0	0	1	1	1	0	0	0	0
EE	0	0	0	0	1	1(0)	0	0	0	0	0
FF	0	0	0	var.	0	0	0	0	0	0	0
GG	0	0	0	0(1)	0	0	0	1	0	0	0
HH	0	0	0	0(1)	0	0	0	1	0	0	0(1)
II	0	0	0	0	1	1	1	0	0	0	0
JJ	1	1	1	1	0	1(0)	0	1	1	1	0
KK	1	1(0)	1	1(0)	1	1	1	0	0	0	0
LL	1	1	1	1	0	0	0	NA	NA	NA	NA
MM	0	0	var.(a)	1a	0	0(1b)	1a	1a	0	0	var.(a,b)
NN	0	0	0	0	0	0	0	0	0	0	1(0)
OO	1	1(0)	1	1	0	0	0	0	0	0	0
PP	0	0(1)	1	0	0	1	1	0	0(1)	1	0
QQ	1	1	1	1	1	0	1	1	1	1	0
RR	0	0	0	0	var.(c)	0	0(1c)	1a	0	0	1b(0)
SS	0	0	0	0	0	0?	0?	0?	0	0?	1
TOTAL	17	16	16	19	16	17	17	16	8	11	12

Leucothoë racemosa and *Lyonia ligustrina* have chartaceous, deciduous leaves and occur in North America at latitudes much farther north than any of the evergreen species within their respective genera. In the Ericaceae, the generalized condition of the leaves seems to be coriaceous

and persistent, but cold-adapted species in a wide range of very distantly related genera have evolved deciduous and much thinner ones. Deciduous leaves occur in some or all of the species of *Arctoüs* Niedz., *Enkianthus* Lour., *Oxydendrum*, *Lyonia*, *Leucothoë*, *Vaccinium* L., *Gaylussacia* H.B.K., *Elliottia* Muhl. ex Ell., and *Rhododendron* L. Similarly, the "heathlike" habit and reduced leaves of *Pieris nana* are probably of adaptive significance in the cold-temperate and alpine situations in which it occurs.

Several interesting developmental inflorescence patterns occur within the Andromedeae. These were first studied by K. Lems (1962), who pointed out that the Ericaceae (which probably originated in a tropical or subtropical climate; see Bell & Burchill, 1955; Wulff, 1946) have a slow morphogenetic cycle, and that such genera as *Pieris*, *Leucothoë*, and *Chamaedaphne*, upon encountering summer-winter climates, have evolved unusual adaptations, including the "overwintering" of dormant and exposed flowers. Other genera, such as *Lyonia*, *Craibiodendron*, *Zenobia*, and *Andromeda*, evolved often large, protective bud scales (modified leaves) to enclose the embryonic inflorescence. The complete development of the inflorescence in the year preceding flowering may allow the plant with this developmental pattern to produce a large, many-flowered inflorescence and still bloom extremely early in the season, since the entire inflorescence and floral structure are already formed, and the flowers have only to open and the stigmas to become receptive for pollination (see Lems, 1962). Several other character states are functionally correlated with this condition, since, if the flower buds are exposed during the winter, the calyx must be modified (i.e., be lengthened to enclose the corolla tightly or be thickened and lignified to protect the internal floral parts). Conversely, the two large, imbricate bud scales of *Lyonia* or *Craibiodendron* provide winter protection for the partially formed inflorescence developing within them, while in *Pieris* or *Leucothoë* such enlarged bud scales are not necessary. The presence of adaxial calyx stomata (and possibly the lack of abaxial corolla stomata) in *Pieris* is also probably correlated with the method of inflorescence development in this genus.

Although winged seeds have arisen independently several times and are probably of adaptive value in dispersal, they are not found in most genera of the Ericaceae. In some species of *Leucothoë* (and *Rhododendron* and *Enkianthus*), cells around the edge of the seed have balloonlike processes that collectively form a fimbriate wing, while in *Pieris floribunda* the seed is flattened and there are small lateral wings of undifferentiated cells (see Stevens, 1969). The very distinctive seeds of *Craibiodendron* have a single large wing (also of cells no different from those covering the body of the seed) on one side. The seeds of this genus are the largest in the *Lyonia* group, and the large wing may enable them to be carried farther by the wind than would otherwise be possible. There is probably less selective pressure for winged seeds in genera with very small, light seeds, such as *Lyonia* or *Agarista*. Other modifications

include the wing of seeds of *Pterospora* Nutt., which is greatly swollen and is produced at the chalazal end of the seed, and the tail of seeds of *Ledum* L., *Menziesia* J. E. Sm., and especially *Rhododendron* sect. VIREYA (see Stevens, 1969). Some species of *Lyonia* sect. LYONIA also have tails at each end of the seed, although they are much smaller. All of these diverse modifications are considered to be evolutionary specializations.

Capsules with prominently thickened (and lignified) sutures that in dehiscence often separate as a unit from the adjacent valves occur only in *Lyonia*, although slightly thickened sutures can be seen in *Enkianthus* and *Oxydendrum* (in which they never separate as a distinct unit). These structures are probably important in seed dispersal, since the capsules are held erect and are persistent, letting the seeds sift out of the cracks between the valves and the sutures over a long period of time. Thus, these thickened and separating sutures are considered to be derived from the typical nonthickened ericaceous capsule-suture, leading to an increased efficiency of the "salt-shaker" mechanism of seed dispersal by wind.

Staminal spurs occur in a scattering of genera throughout the Ericaceae; for example, in the Vaccinioideae they are found in *Andromeda*, *Pieris*, and *Lyonia* of the Andromedeae, in such genera as *Vaccinium*, *Dimorphanthera* F. Mueller, and *Psammisia* Klotzsch of the Vaccinieae, in *Cassiope* D. Don and *Harrimanella* Cov. of the Cassiopeae, and in such genera as *Arctostaphylos* Adanson and *Arbutus* L. of the Arbuteae. They are also common in the Ericoideae and the Monotropoideae. The spurs of these various groups are morphologically diverse — for example, flattened in the Ericoideae, robust in many Vaccinieae and Arbuteae, and slender and fragile in *Lyonia*. Their position varies (they can arise from either the filament as in *Lyonia*, the anther-filament junction as in *Pieris*, or the anther connective tissue beyond the point of union of anther and filament as in many Vaccinieae), and they can be paired structures, which is the usual condition, or single structures, as in *Anthopteropsis* A. C. Sm. and some species of *Dimorphanthera* (Stevens, 1969; pers. obs.). It thus seems likely that spurs may have some adaptive significance, probably related to the pollination mechanism, and have evolved independently (and secondarily become lost and regained) in many different groups within the family. This argument is reinforced by the fact that species with exserted stamens (and thus with a very different pollination mechanism) are usually devoid of spurs (see Artopoeus, 1903; Matthews & Knox, 1926; and Stevens, 1971). The slender, geniculate filaments and/or spurs of the *Lyonia* group probably act as an obstacle to the proboscis of pollinators, causing pollen to be sifted out of the anthers, and are thus functionally important in the pollination biology of these species. It is interesting that taxa with geniculate filaments, with the exception of *Pieris phillyreifolia*, tend to lack stout spurs. Therefore, it is possible that the presence of one structure (geniculate filaments) makes the second (spurs) functionally redundant, and it is of interest that in *Lyonia*, which has both geniculate filaments and

spurs, the spurs are usually rather small and fragile and are possibly nonfunctional. Spurs may have been acquired early in the evolution of the *Lyonia* group (as evidenced by their presence in both *Lyonia* and *Pieris*) but were subsequently lost in many taxa that developed geniculate filaments (*Craibiodendron*, *Agarista*, and *Agauria*).

The interrelationships of the various inflorescence types and the probable primitive condition will be discussed in detail in a later paper, but the inflorescence of *Craibiodendron*, which possesses terminal flowers, is likely primitive within the Andromedeae (see Weberling, 1965).

Several additional character states probably also developed through selective pressures relating to their functions, but the nature of these interactions is less well known. These include superposed (supernumerary) buds; the presence of a dense covering of unicellular hairs on the abaxial leaf surface; the presence of peltate scales; 4-, 6-, or 7-merous flowers; campanulate and/or carnose corollas; and pseudoverticillate or whorled leaves. Superposed buds occur only in *Craibiodendron*, where both buds produce paniculate inflorescences. The dense layer of unicellular hairs on the abaxial leaf surface of many species of *Lyonia* sect. LYONIA and of *Agarista mexicana* var. *pinetorum* [2] may function in retarding water loss. The lepidote indumentum of *Lyonia* sect. LYONIA possibly protects the growing shoots from water loss, extremes of temperature, or over-heating due to solar radiation. The campanulate and carnose corollas of *Craibiodendron* are probably important in the pollination biology of that genus. Fleshy (or carnose) corollas occur also in some species of *Rhododendron*, a few species of *Lyonia* sect. LYONIA, and several tropical genera of Vaccinieae. The increased (or decreased) number of flower parts observed in some lyonias (especially *Lyonia* sect. LYONIA) may be a means of increasing (or decreasing) the number of seeds produced, or it may be the result of selection for larger (or smaller) flowers. Finally, pseudoverticillate leaves, which occur in such diverse genera as *Rhododendron*, *Agapetes* D. Don ex G. Don, and *Pieris*, probably affect the photosynthetic capability of the plant (see Horn, 1975).

The following character states were considered derived at least in part because they are uncommon either within the *Lyonia* group or in the Ericaceae as a whole (i.e., they are found in only a single taxon or in only a few phenetic groups): bud scales imbricate, 2 large or 3; buds superposed; attachment of bud to twig elongate; habit low, "heathlike"; fiber bands present in phloem of older twigs; leaves pseudoverticillate or whorled; node of three traces from one gap; leaves deciduous; leaves less than 1.5 cm. long; leaves revolute in bud; leaf epidermal cells divided;

[2] This taxon and its relatives have usually been included in *Leucothoë* and were referred to by Sleumer (1959) as *Leucothoë* sect. *Agastia*; see also Stevens (1970). The following new combinations are made here: **Agarista mexicana** (Hemsley) Judd var. **mexicana**, comb. nov. (*Andromeda mexicana* Hemsley, Biol. Centr.-Am. Bot. 2: 282. 1881); **Agarista mexicana** (Hemsley) Judd var. **pinetorum** (Standley & Williams) Judd, comb. nov. (*Leucothoë pinetorum* Standley & Williams, Ceiba 3: 54. 1952); and **Agarista populifolia** (Lam.) Judd, comb. nov. (*Andromeda populifolia* Lam. Encycl. Méth. Bot. 1: 159. 1783).

leaf hypodermis present; all veins of leaf (except midvein) more or less equally prominent and densely reticulate; stomata paracytic; abaxial leaf epidermis papillose or densely covered with unicellular hairs; indumentum of peltate scales; multicellular hairs with elongated heads; multicellular hairs with more or less large, swollen heads; bracteoles strictly basal or tending to be near apex of pedicel; flowers 4-, 6-, or 7-merous; corolla more or less campanulate, fleshy; abaxial corolla stomata absent; staminal spurs with disintegration tissue; anthers with awns; capsules with thickened sutures; placentae basal; and chromosome numbers other than $x = 12$.

It is difficult to defend uncommonness as a criterion of advancement when only the within-group distribution of a character is considered, since the distribution of character states depends upon the phylogeny of the group and where within the sequence a particular character changes. Thus, this criterion was used in conjunction with other lines of evidence and then only after a comprehensive examination of the pattern of variation within the Andromedeae and Vaccinioideae.

Finally, several character states are rather arbitrarily considered to be derived because they seem to be correlated with one or more of the derived character states described above. They are: vascular bundle of petiole and leaf midrib bifacial; leaves with free fibers in the mesophyll; leaves serrulate or serrate; multicellular hairs with biseriate stalks; calyx lobes valvate in bud; filaments papillose; seed coat cells strongly elongated.

The Wagner Tree (FIGURE 2) resulting from the above procedure depicts the same five groups indicated by the phenetic analysis. These five groups are listed below along with the derived character states commonly present in or characteristic of each group. The characters listed for each group include some that are unique to and constant or nearly constant within the group, indicated by a double asterisk (**); some that are unique to the group but are only found in some species, indicated by a single asterisk (*); some that are not unique to the group but are constant within it, indicated by a double dagger (‡); and some that are neither unique to nor constant within the group, indicated by a single dagger (†).

The *Pieris* group is designated by the following derived characters: B (fiber bands in phloem)‡, Q (leaf epidermis often lignified)†, V (multicellular hairs usually with biseriate stalks)‡, AA ("overwintering" of nearly mature flower buds)‡, BB^b (bracteoles often positioned near apex of pedicel)‡, CC (calyx lobes valvate)‡, DD (sepals with prominent fiber strands)**, II (abaxial corolla stomata lacking)**, KK (spurs present)‡, and QQ (seed coat cells elongated, lost in *Pieris* sect. PHILLYREOIDES)†.

The genus *Lyonia* is characterized by the following derived characters: B (fiber bands in phloem)‡, D^a (buds usually with 2 imbricate scales)†, R (vascular bundle of petiole bifacial)‡, V (multicellular hairs with biseriate stalks)‡, X (multicellular hairs with large, swollen heads)**,

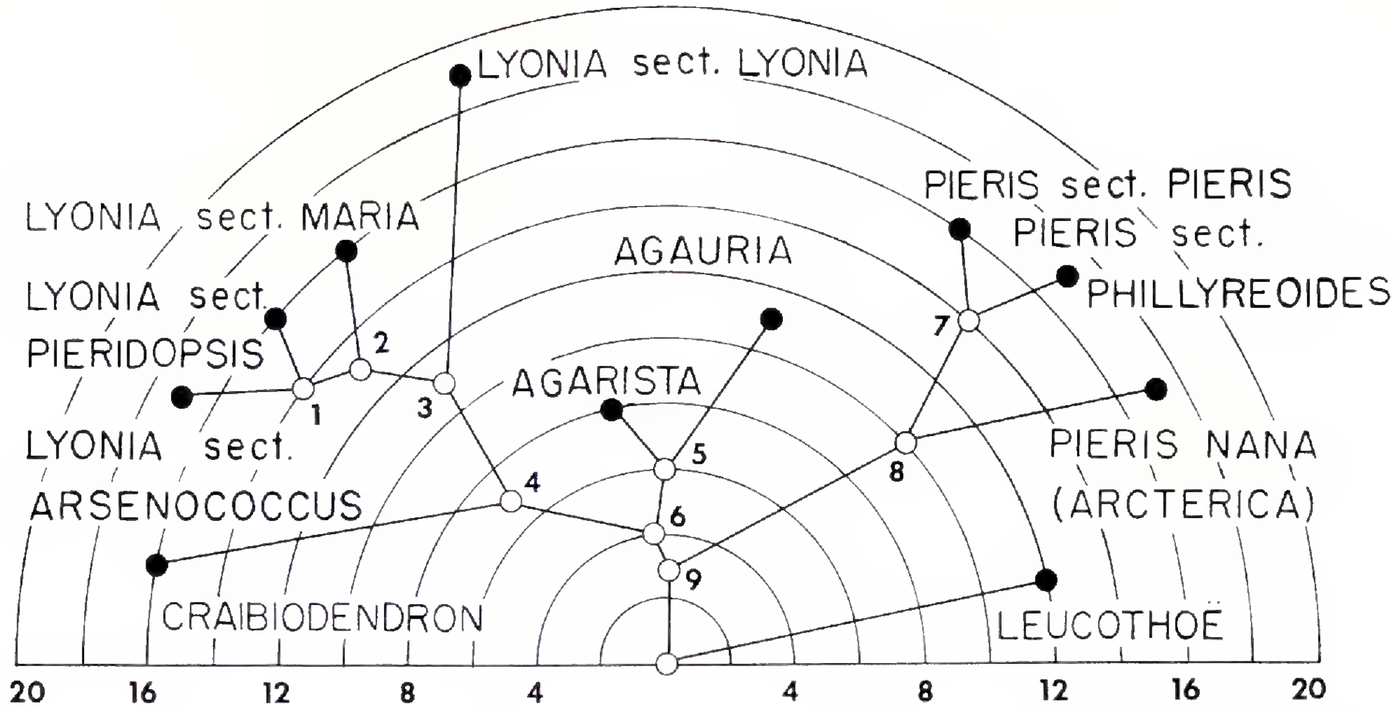

FIGURE 2. Wagner Tree for the genera of the *Lyonia* group of the Andromedeae (also including *Leucothoë*): present day taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally in tree (open circles). Derived character states for each taxon: *Craibiodendron* — B, D^a, E, F, I, N, P, Q, R, V, GG, HH, JJ, MM^a, QQ, RR^a; *Lyonia* sect. ARSENOCOCCUS — B, C^a, D^a, H, L, R, V, X, Y, Z^a, BB^a, CC, JJ, KK, LL, OO, QQ; *Lyonia* sect. PIERIDOPSIS — B, D^a, H, R, T, V, X, Y, Z^b, BB^a, CC, JJ, KK, LL, OO, QQ,; *Lyonia* sect. MARIA — B, D^c, H, R, V, X, Z^c, BB^a, CC, JJ, KK, LL, MM^a, OO, PP, QQ; *Lyonia* sect. LYONIA — B, D^a, L, P, Q, R, U, V, W, X, Z^c, BB^a, FF, JJ, KK, LL, MM^a, OO, QQ; *Agarista* — B, C^b, M, O, Q, Z^b, JJ, QQ; *Agauria* — B, C^a, J, M, P, Q, T, Z^b, JJ, PP, QQ; *Pieris* sect. PIERIS — B, C^a, G^a, L, Q, V, Z^d, AA, BB^b, CC, DD, EE, II, KK, QQ, RR^b; *Pieris* sect. PHILLYREOIDES — B, C^a, F, G^a, L, Q, V, Z^b, AA, BB^b, CC, DD, EE, II, JJ, KK, PP; *Pieris* (*Arcterica*) *nana* — A, B, D^b, G^b, K, Q, V, Z^e, AA, BB^b, CC, DD, II, KK, MM^a, PP, QQ; *Leucothoë* — $C^{a,b}$, F, H, L, S, Z^b, AA, BB^b, $MM^{a,b}$, NN, RR^b, SS. For hypothetical ancestors: 1 — B, D^a, H, R, V, X, Y, BB^a, CC, JJ, KK, LL, OO, QQ; 2 — B, D^a, H, R, V, X, BB^a, CC, JJ, KK, LL, OO, QQ; 3 — B, D^a, R, V, X, BB^a, JJ, KK, LL, OO, QQ; 4 — B, D^a, R, V, JJ, KK, QQ; 5 — B, M, Q, Z^b, JJ, QQ; 6 — B, JJ, KK, QQ; 7 — B, C^a, G^a, L, Q, V, AA, BB^b, CC, DD, EE, II, KK, QQ; 8 — B, Q, V, AA, BB^b, CC, DD, II, KK, QQ; 9 — B, KK, QQ.

BB[a] (bracteoles basal or nearly so)**, JJ (filaments geniculate)‡, KK (spurs present)‡, LL (spurs with disintegration tissue)**, OO (capsules with strongly thickened sutures)**, and QQ (seed coat cells very elongated)‡.

Craibiodendron possesses the following derived characters: B (fiber bands in phloem)‡, D[a] (buds with 2 imbricate scales)‡, E (superposed buds)**, F (buds with elongated attachment to twig)‡, I (node often with three traces from one gap)*, N (fibers in leaf mesophyll)*, P (leaves often with hypodermis)†, Q (leaf epidermis lignified)‡, R (vascular bundle of petiole bifacial)‡, V (multicellular hairs with biseriate stalks)‡, GG and HH (corolla more or less campanulate and fleshy)**, JJ (filaments geniculate)‡, MM[a] (filaments roughened-papillose)‡, QQ (seed coat cells very elongated)‡, and RR[a] (seeds with single large wing on one side)**.

The *Agarista-Agauria* group shares the following derived characters: B (fiber bands in phloem)‡, M (veins of leaves densely reticulate with all veins more or less equally prominent)**, Q (leaf epidermis lignified)‡, Z[b] (racemes, terminal flowers lacking)‡, JJ (filaments geniculate)‡, and QQ (seed coat cells very elongated)‡.

The genus *Leucothoë* is distinguished by: C[a,b] (some species with heterogeneous or *Calluna*-type (i.e., with small cells around the outside and larger cells in the center) pith; see Stevens, 1970)†, F (buds of some species with elongated attachment to twig)†, H (some species with deciduous leaves)†, L (leaves serrate)‡, S (stomata paracytic)**, Z[b] (racemes, terminal flowers lacking)‡, AA (inflorescences exposed for some time before flowering)‡, BB[b] (bracteoles at apex of pedicel in some species)†, MM[a,b] (some species with papillose filaments, others smooth)†, NN (several species with awns)*, RR[b] (some species with winged seeds, derived from balloonlike outgrowths of individual cells)*, and SS (chromosome number, where known, of $x = 11$)**.

Several examples of the loss of a derived character within a group are revealed. One is the probable loss of spurs in *Craibiodendron*, *Agauria*, *Agarista*, and a few species of *Lyonia*; a second is the loss (in all but an occasional leaf) of the bifacial midrib bundle in *Lyonia lucida*. *Pieris cubensis*, *P. phillyreifolia*, and *P. swinhoei* (*Pieris* sect. PHILLYREOIDES) have lost the elongated seed coat cells that probably characterized their ancestors and that are still present in *P. japonica*, *P. formosa*, *P. floribunda* (*Pieris* sect. PIERIS) and *P. nana*. The lack of epidermal lignification in the leaves of many individuals of *Lyonia ligustrina* (sect. ARSENOCOCCUS), *L. lucida* and *L. mariana* (sect. MARIA), and in *Lyonia* sect. PIERIDOPSIS is probably a reversal of the derived condition (epidermis lignified), which is the common condition in the *Lyonia* group of genera.

A few examples of parallel evolution of characters are also evident within this group. Some of the more interesting are: the presence of biseriate-stalked multicellular hairs in *Pieris* and *Lyonia/Craibiodendron;* the heterogeneous pith of *Lyonia* sect. ARSENOCOCCUS, *Pieris*, and *Agauria;* the serrate or serrulate leaves of many species of *Lyonia* sects. LYONIA

and ARSENOCOCCUS, *Pieris*, and *Agarista populifolia*; the papillae that densely cover the abaxial leaf surface of *Agauria* and a few species of *Lyonia* sect. PIERIDOPSIS; the dense covering of unicellular hairs on the abaxial leaf surface of *Agarista mexicana* var. *pinetorum* and many species of *Lyonia* sect. LYONIA; the basal placentae of *Agauria* and *Pieris* sect. PHILLYREOIDES, and the often nearly basal placentae of *Lyonia* sect. MARIA; the papillose or roughened filaments of *Craibiodendron*, *Lyonia* sect. LYONIA, *Lyonia lucida*, and *Pieris nana* (in most cases probably due to the loss of long unicellular hairs), and the geniculate filaments of *Pieris phillyreifolia* and *Lyonia/Craibiodendron/Agarista/Agauria*. Another example, although not evident from this phylogenetic analysis, is the presence in a few species of small, extremely revolute leaves in both *Agarista* and *Lyonia* sect. LYONIA. There are also many examples of parallel evolution between *Leucothoë* and the genera of the *Lyonia* group. These can be easily determined by scanning TABLE 4 for any "supposed" shared derived characters. If the function of these characters were more clearly understood, or if the evolutionary history of the group were better known, this situation could probably be readily explained.

The results of the cladistic analysis (see FIGURE 2) also indicate a relationship between *Craibiodendron*, *Agauria* and *Agarista*, and *Lyonia*. These taxa all have geniculate filaments and very elongated seed coat cells. All have abaxial corolla stomata, and embryonic inflorescences that "overwinter" within protective bud scales; all lack prominent fiber strands in the calyx lobes. In addition, *Craibiodendron* and *Lyonia* both have buds with two imbricate bud scales and a bifacial leaf midrib bundle. These four genera form an evolutionary line perhaps weakly distinct from *Pieris*, which has inflorescences that develop in the year preceding flowering and are thus exposed during the winter, prominent fiber strands in the calyx, corollas that lack stomata on the abaxial surface, and usually straight filaments. All five genera have fiber bands in the phloem of the branches. Thus, the results do seem to support the hypothesis that *Lyonia*, *Craibiodendron*, *Agarista*, *Agauria*, and *Pieris* form a related group of genera. This *Lyonia* group is best characterized by the presence of fiber bands in the phloem, but other useful characters include the elongated seed coat cells, the geniculate filaments and/or spurs, and a tendency toward epidermal lignification.

The phylogenetic isolation of *Leucothoë* is demonstrated by this cladistic study, although it was not evident from the phenetic investigation (using an almost identical set of characters) due to the many cases of parallel evolution of characters between the two groups. This parallel evolution is possibly the result of similar selective pressures on groups with quite similar genetic backgrounds. The cladistic distinctiveness of *Leucothoë* is especially expressed by the presence of awns (in several species) and paracytic stomata, by a chromosome number of $x = 11$, and by the lack of fiber bands in the phloem and elongated testa cells. FIGURE 2 supports the phenetic study in its close grouping of *Agarista* and *Agauria*, two taxa that should undoubtedly be considered as a single

genus. The low level of advancement of these two taxa made them appear rather more similar to *Leucothoë* in the phenetic study than the phylogenetic analysis has shown them to be because both *Agarista/Agauria* and *Leucothoë* have retained several primitive character states (that have often been variously modified in related genera). For example, both groups have two small bud scales that soon open (as the bud develops) to reveal several additional scales (D); alternate and more or less equally spaced leaves (G) with a unifacial midrib vascular bundle (R); multiseriate-stalked multicellular hairs (U) with small, round, glandular heads (X and Y); imbricate calyx lobes (CC); urceolate to cylindrical, 5-merous, thin corollas (FF, GG, and HH); abaxial corolla stomata (II); and capsules with unthickened sutures (OO). In addition, both lack adaxial corolla stomata (EE) and filament spurs (KK). Thus, much of their phenetic similarity (see FIGURE 1) is due to many shared primitive characteristics. As in the phenetic treatment, *Pieris nana* is shown to be most closely related to the species of *Pieris* sects. PIERIS and PHILLYREOIDES and could be treated as an isolated and monotypic subgroup of this genus.

CONCLUDING COMMENTS

It seems most in accordance with the results of both phenetic and phylogenetic analyses to recognize four monophyletic groups within the *Lyonia* group of genera, one leading to *Agauria* and *Agarista*, one to *Craibiodendron*, one to *Lyonia*, and one to *Pieris* (including *Pieris nana*). In addition, the fundamental separation between the *Lyonia* and *Gaultheria* groups is supported if *Leucothoë* can be taken as typical of the latter.

Even if the relationships illustrated in FIGURE 2 were completely accurate, it would not remove all the arbitrary aspects of the determination of generic limits. However, it would allow one to be more consistent in the application of characters and to estimate the taxonomic "usefulness" of any given character within the group in question. In the *Lyonia* group of the Andromedeae, it seems least arbitrary and most informative of evolutionary relationships to consider each of the four major evolutionary lines at the generic level, with their ultimate branches as either sections or subgenera (see Hall & Clements, 1923).

ACKNOWLEDGMENTS

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NOTES ON THE GENUS POLYGALA IN THE UNITED STATES AND MEXICO

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A MONOGRAPH of *Polygala* L. section RHINOTROPIS Blake has recently been completed and is being prepared for publication. The purpose of the present article is to validate a number of nomenclatural changes and to note taxonomic reinterpretations in this section before publication of the revised edition of the National List of Scientific Plant Names. In order to present a complete picture of the proposed changes, Mexican taxa that do not occur in the United States are included when relevant to the discussion of United States taxa. In addition, *Polygala watsonii* Chodat of section MONNINOPSIS Gray is reported as new to the United States.

Polygala section RHINOTROPIS Blake, Contr. Gray Herb. 47 : 70. 1916.

Polygala heterorhyncha (Barneby) Wendt, comb. et stat. nov.

Polygala subspinosa S. Watson var. *heterorhyncha* Barneby, Leafl. W. Bot. 3: 194. 1943. TYPE: United States. Nevada. Southeastern Nye Co., foothills of Spotted Range, toward Frenchman Flat, *Ripley & Barneby 3427* (CAS!, holotype; GH!, isotype).

This taxon has been treated as a variety of *Polygala subspinosa* S. Watson, and Beatley (1976) states that it is "doubtfully distinct" even at that rank. However, where the range of the widespread *P. subspinosa* approaches that of the local *P. heterorhyncha* in southern Nevada, these taxa show no intergradation in the key characters given below and are strongly separated ecologically. In this area, *P. subspinosa* is confined to juniper and pinyon-juniper woodlands and sagebrush desert at 1600–2000 meters in the volcanic uplands to the north, while *P. heterorhyncha* is found in Mojave Desert scrub and less frequently in transitional desert vegetation (e.g., *Coleogyne* scrub) at 900–1525 meters in the valleys to the south (see Beatley, 1976, for a review of the vegetation of this area). The two species may be separated by the following key.

Beak of keel petal entire or slightly erose; body of seed more or less evenly and moderately densely pubescent or infrequently with glabrate patches. ..... *P. subspinosa.*

Beak of keel petal with 1 or 2 prominent invaginations along lower side formed by sinuate excess tissue; body of seed densely pubescent just below umbo of aril, lower half sparsely and unevenly pubescent to glabrate. ..... *P. heterorhyncha.*

Polygala intermontana Wendt, stat. et nom. nov.

Polygala acanthoclada Gray var. *intricata* Eastwood, Proc. Calif. Acad. Sci. II. **6**: 283. 1896, non *P. intricata* Blake. TYPE: United States. Utah. San Juan Co., Willow Creek, 14 July 1895, *Eastwood 10* (in part) (CAS!, holotype; GH!, UC!, isotypes). Paratype: United States. Utah. San Juan Co., Barton's Range, 13 July 1895, *Eastwood 10* (in part) (MO!, US!).

This Great Basin species is distinguished from the more southern *Polygala acanthoclada* Gray by the characters given in the key below. Both species are diploid, $n = 9$ (Wendt, unpubl.); the few morphological intermediates found in the limited zone of sympatry in southeastern Utah and northern Arizona are tetraploid, $n = 18$. These facts argue strongly for recognition of the two taxa as separate species, which can be separated by the key that follows.

Leaves and branchlets densely pubescent with spreading hairs; pedicels pubescent, usually shorter than flowers, 1.5–4.0(–5.8) mm. long; outer sepals pubescent with spreading hairs. . . . . *P. acanthoclada.*

Leaves densely pubescent with incurved hairs; branchlets with densely matted or shaggy tomentum of appressed, incurved, or occasionally irregularly inclined or divergent hairs; pedicels glabrous, usually longer than flowers, (2.5–)3.0–7.0(–9.0) mm. long; outer sepals glabrous or merely ciliate, occasionally with a few incurved hairs near apex. . . . . *P. intermontana.*

The taxa related to *Polygala lindheimeri* Gray have long been a perplexing problem. This complex is distinguished by the following suite of characters: upper sepal alone persistent in fruit, keel prominently beaked and/or saccate portion of keel glabrous, wings rose-pink, racemes typically leaf-opposed. Blake, the last monographer of the North American members of the genus, varied in the number of species that he recognized within this complex from nine (1916) to four (1924). Barneby (1970) noted that it is "a critical group. . . . Specific lines are hard to draw, for the available differential criteria are seldom absolute."

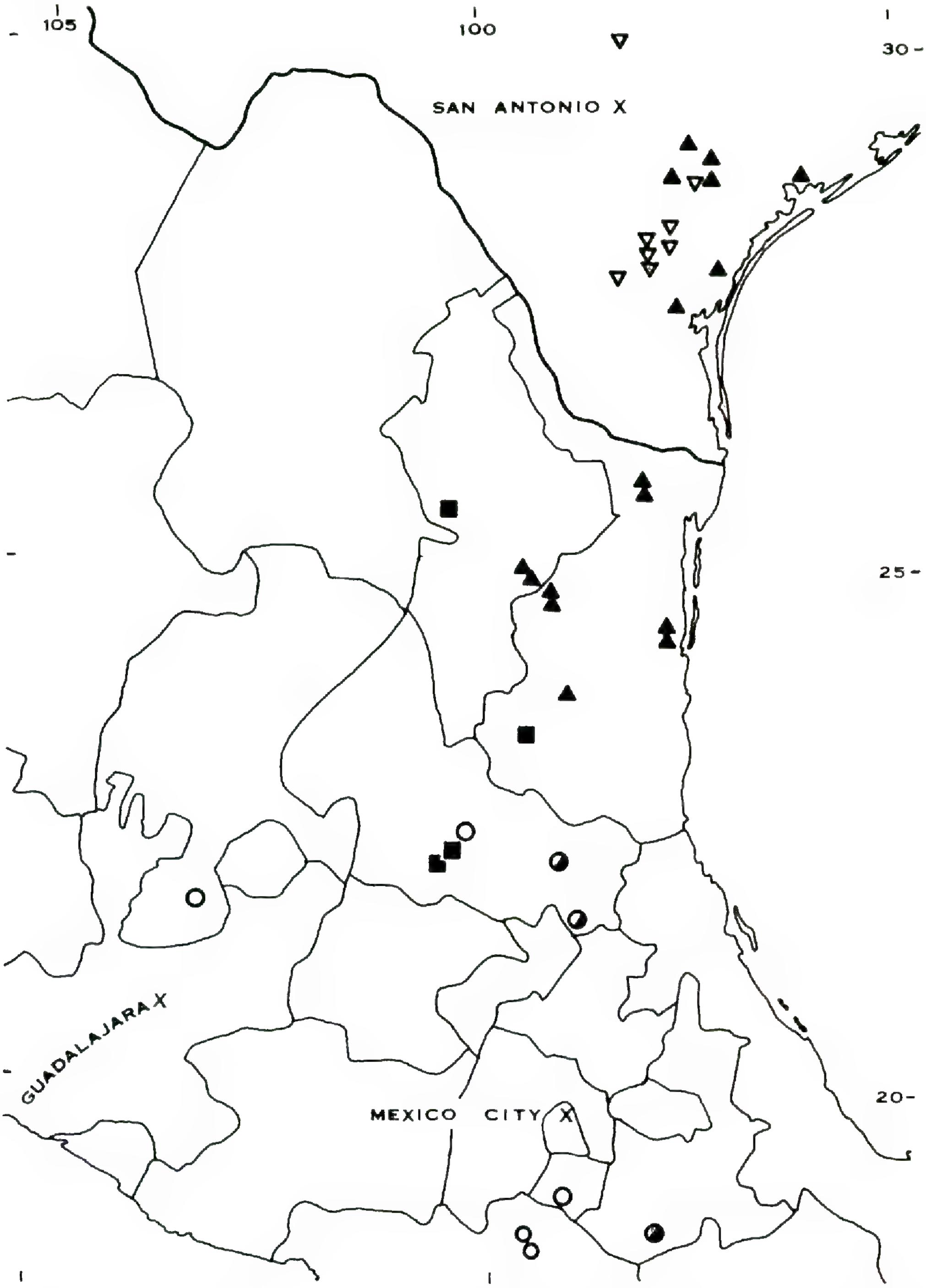
In the present treatment I recognize two species, each with a number of varieties (MAPS 1, 2). Justification for this decision and full synonymy will be given in the monograph to follow. The two species may be distinguished by the following key.

Rootstock with prominent, bright orange-red cortex loosely exfoliating in thin layers; stamens 8 or 7; [chromosome number $n = 18$ or 27]. . . . *P. nitida.*

Rootstock with firm, brown, gray, or dull red-brown cortex not exfoliating in thin layers; stamens 7; [chromosome number $n = 9$ or 18 ($n = 9$ in U. S. taxa)]. . . . . *P. lindheimeri.*

Polygala nitida T. S. Brandegee, Univ. Calif. Publ. Bot. **4**: 272. 1912. TYPE: Mexico. San Luis Potosí. Minas de San Rafael, Bagre, *Purpus 5168* (UC!, holotype; BM (*fide* Blake, 1916), F!, GH!, NY!, US!, isotypes).

Polygala nitida, previously treated as confined to Mexico, is here considered to be composed of four varieties, two of which occur in the United States (MAP 1). Jones (1975) apparently referred South Texas populations of both of the United States taxa to *P. tweedyi* Britton ex Wheelock



MAP 1. Distribution of *Polygala nitida* var. *nitida* (squares), var. *lithophila* (circles), var. *tamaulipana* (closed triangles), var. *goliadensis* (open triangles); intermediates between var. *lithophila* and other varieties (half-circles).

(= *P. lindheimeri* var. *parvifolia* Wheelock), although he cited no collections. The varieties of *Polygala nitida* may be separated by the following key.

A. Flowers 3.4–5.0(–5.3) mm. long; beak 0.2–0.6 mm. long, deltoid or oblong, less (usually much less) than twice as long as thick, or occasionally absent; stamens 7; [chromosome number $n = 18$]. ..... var. *lithophila*.

A. Flowers (4.1–)4.5–7.5 mm. long; beak (0.6–)0.8–1.7 mm. long, oblong to linear, two or more times as long as thick, or rarely absent; stamens 7 or 8; [chromosome number $n = 18$ or 27].

B. Flowers (4.1–)4.5–6.1 mm. long; leaves mostly suborbicular, obovate or elliptic, the apex rounded or obtuse, abruptly mucronate, infrequently acute in distal leaves; distal leaves similar to lower or, when distinctly narrower, usually narrowly obovate; beak white or yellow, with or without rose on tip; stem pubescent with closely incurved hairs 0.07–0.15 mm. long; stamens 8; [chromosome number $n = 18$]. ..... var. *nitida*.

B. Flowers (4.4–)5.0–7.5 mm. long; leaves linear, ovate, or elliptic, apex acute to acuminate, extended gradually into mucronate tip, less frequently rounded and abruptly mucronate; distal leaves, when distinctly narrower than basal, lance-ovate to linear; beak white to yellow, usually rose along lower side throughout; stem pubescence as in var. *nitida*, or hairs loosely incurved and longer; stamens 7 or 8; [chromosome number $n = 18$ or 27].

C. Leaves, including basal ones, narrowly elliptic (at least 5 times as long as wide), lanceolate, or linear (or, when leaves in lower third of stem broader, then the distal leaves lance-elliptic, much narrower than basal, and stem pubescence of closely incurved-appressed hairs mostly 0.07–0.15(–0.2) mm. long, these lying very close to stem surface with free tip touching stem); [chromosome number $n = 18$]. ..... var. *tamaulipana*.

C. Leaves in lower third of stem elliptic to ovate, 1.5–3 times as long as wide, distal leaves similar or somewhat narrower but never lanceolate or linear; stem pubescence mostly of loosely incurved hairs 0.15–0.3 mm. long, the hair tips not close to stem surface; [chromosome number $n = 27$]. ..... var. *goliadensis*.

Polygala nitida T. S. Brandegee var. **lithophila** (Blake) Wendt, comb. et stat. nov.

Polygala lithophila Blake, Contr. Gray Herb. **47**: 74. 1916. TYPE: Mexico. San Luis Potosí. Minas de San Rafael, Guascamá, *Purpus 5175* (GH!, holotype; NY!, UC!, isotypes).

Polygala erythrorrhiza Barneby, Rhodora **72**: 69. 1970. TYPE: Mexico. Guerrero. 11 mi. S. of Iguala, 2600 feet, *Ripley & Barneby 13737* (NY!, holotype; CAS!, K (*fide* Barneby), MICH!, US (*fide* Barneby but not located there by author), isotypes).

This taxon is known from scattered localities in San Luis Potosí, southern Zacatecas, Morelos, and Guerrero; collections from eastern San Luis Potosí are morphologically intermediate between *Polygala nitida* vars. *nitida* and *lithophila*, and a single collection from southern Puebla shows affinities to the quite allopatric *Polygala nitida* var. *tamaulipana*

(MAP 1). It is usually found on soft or crumbly, often highly mineralized soils at 325–1500 meters elevation in tropical deciduous scrub.

Polygala nitida T. S. Brandegee var. **nitida.**

The typical variety is known from a few localities in the Sierra Madre Oriental from San Luis Potosí to Nuevo León (MAP 1). Its usual habitat is deep but rocky, calcareous or shaley soils at 1200–1800 meters, in subtropical oak woodland or occasionally in juniper woodland.

Polygala nitida T. S. Brandegee var. **tamaulipana** Wendt, var. nov.

Polygala lithophila Blake, *pro parte*, but not as to type.

Planta erecta 5–20 cm. alta; caules arcte incurvati-puberuli pilis 0.07–0.1(–0.15) mm. longis. Folia lanceolata vel linearia vel anguste elliptica, interdum folia inferna latiora, 0.5–3.5(–4.0) cm. longa, 0.1–0.3 cm. lata (folia inferna interdum ad 0.8 cm. lata), plerumque firma; apex acutus vel acuminatus sensim mucronatus. Pedicelli 1.5–3.0 mm. longi; flores (4.4–)5.0–7.5 mm. longi; sepala inferna plerumque viridia ad marginem dilute rosea vel alba; rostrum carinae (0.6–)0.8–1.7 mm. longum (raro deficiens) oblongum vel lineare, omnino album vel luteum, vel latus infernum roseum vel tantum apex roseus; stamina 7 vel 8. Capsula subsessilis vel perbrevistipitata, basis rotundata vel acuta. Chromosomatum numerus $n = 18$.

TYPE: Mexico. Tamaulipas. 45 mi. N. of San Fernando (29 mi. N. of jct. of Rtes. 100 & 97) along Rte. 97 to Reynosa, ca. 46 mi. S. of Reynosa, 25°26′ N., 98°13′ W., ca. 75 m. elevation, roadside in nearly flat caliche brushland, 1 August 1977, *Wendt 2095* (holotype, LL; isotypes, ENCB, MEXU). Chromosome number of type population $n = 18$.

The new variety is known from central Tamaulipas and eastern Nuevo León northward near the coast into the eastern part of South Texas, reaching as far north as Lavaca Bay and DeWitt County (MAP 1). It is generally found on dry soils from near sea level to 600 meters elevation, in Tamaulipan thorn scrub, oak savanna, and coastal prairie, or occasionally in montane woodland. Some Mexican populations show intergradation to *Polygala nitida* var. *nitida*.

REPRESENTATIVE SPECIMENS. **Mexico.** NUEVO LEÓN: 11 mi. E. of Linares on road to Guadalupe, *M. C. Johnston & Graham 4254A* (TEX). TAMAULIPAS: 3 mi. W. of Morales, 19 mi. E. of Matamoras–Victoria highway on the road to Loreto, *Johnston & Crutchfield 5350* (MICH, TEX). **United States.** TEXAS: Calhoun Co., Port Alto, 25 July 1937, *Drushell s.n.* (NY); Goliad Co., 1.8 mi. SE of Weesatche, *Wendt 1972* (LL); Kleberg Co., Kingsville, *Tracy 9427* (GH, MO, NY); San Patricio Co., 7½ mi. S. of Taft, *F. Jones 469* (SMU).

Polygala nitida T. S. Brandegee var. **goliadensis** Wendt, var. nov.

Planta effusa vel fere erecta 5–20 cm. alta et usque 20 cm. lata plerumque multo parvior; caules laxe incurvate-puberuli, pilis pro parte maxima

0.15–0.3 mm. longis. Folia elliptica vel ovata, interdum folia distalia angustiora, 0.8–2.2(–2.5) cm. longa, (0.2–)0.3–0.9 cm. lata, plerumque firma et reticulata; apex acutus et sensim mucronatus vel interdum rotundatus et abrupte mucronatus. Pedicelli (2.0–)2.5–4.0 mm. longi; flores (4.6–) 5.0–7.3 mm. longi; sepala inferna plerumque viridia ad marginem dilute rosea vel alba; rostrum carinae (0.6–)0.8–1.7 mm. longum, oblongum vel lineare, album vel luteum, et plerumque roseum in latere inferno; stamina 7 vel 8. Capsula sessilis basi acuto vel rotundato, vel brevistipitata stipite 0.3–0.5 mm. longo. Chromosomatum numerus $n = 27$.

TYPE: United States. Texas. Duval Co., 19.1 mi. ESE. of Freer on Rte. 44, 5.4 mi. ESE. of jct. with Rte. 3196 to Rosita, 27°47′15″ N., 98°20′30″ W., ca. 450 ft. elevation, low caliche cut along highway, crumbly open slope, 19 July 1977, *Wendt 1978* (holotype, LL; isotypes, MEXU, SMU). Chromosome number of type population $n = 27$.

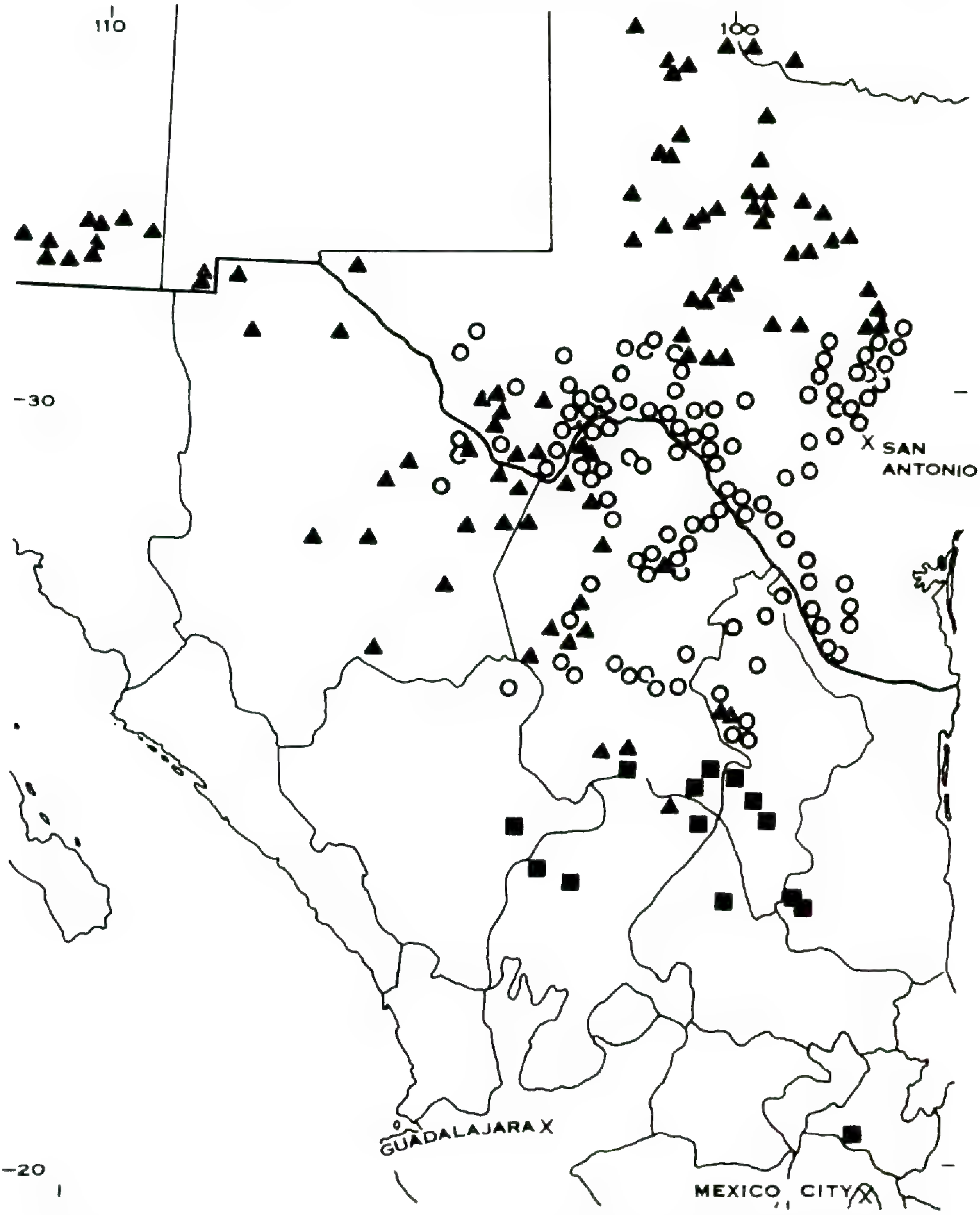
Polygala nitida var. *goliadensis* is known from the central part of South Texas in Duval, Wells, Live Oak, San Patricio, Bee, and Goliad counties, and from an apparently disjunct population in Blanco County in the central part of the state (MAP 1). Through most of its range, it inhabits Tamaulipan thorn scrub at 50–150 meters elevation; the Blanco County population is in an area of Edwards Plateau juniper-oak woodland at ca. 300 meters elevation. The new variety is most common on crumbly, open slopes and roadcuts of the Goliad Formation of South Texas (Jones, 1975), from which it draws its name. Toward the coast from this formation, *P. nitida* var. *goliadensis* is replaced by *P. nitida* var. *tamaulipana*; a narrow zone exists in which apparent intergrades are found.

REPRESENTATIVE SPECIMENS. **United States.** TEXAS: Bee Co., 8.0 mi. W. of center of Beeville on U. S. Rte. 59, *Wendt 2097* (LL); Blanco Co., Blanco, dry open ground, *E. J. Palmer 12155* (MO, NY, POM, UC); Goliad Co., 4.5 mi. W. of Goliad on Rte. 239, *Wendt 2098* (LL); San Patricio Co., 2.1 mi. NW. of Mathis, *W. Lewis & F. Jones 5583* (MO).

Polygala lindheimeri Gray, Boston J. Nat. Hist. 6: 150. 1850. LECTOTYPE (here designated): United States. Texas. "On rocks, Pierdenales 6/47," *Lindheimer exsic. fasc. III no. 333 field no. 498* (GH!). Paratypes: United States. Texas. "Rocky declivities of the Upper Guadaloupe, Aug. 1845," *Lindheimer exsic. fasc. III no. 333 field no. 500* (GH (2 sheets)!, MO!); "Rio Grande East to Colorado on rocky hills," *Wright s.n.* (GH!). Blake (1916) cited a specimen of the *Lindheimer III. 333* at BM, but a field number (if present) was not given.

Polygala lindheimeri includes three varieties, two of which occur in the United States (MAP 2). They may be distinguished by the following key.

A. Plant pubescent with spreading hairs 0.3–0.5 mm. long, rarely glabrous; lower leaves elliptic, ovate, or obovate, usually prominently reticulate, firm; distal leaves often narrower than basal ones but rarely lanceolate; [chromosome number $n = 9$]. ..... var. *lindheimeri*.



MAP 2. Distribution of *Polygala lindheimeri* var. *lindheimeri* (circles), var. *parvifolia* (triangles), var. *eucosma* (squares).

A. Plant pubescent with incurved hairs 0.07–0.15(–0.2) mm. long, rarely entirely glabrous but leaves frequently so; leaves as in var. *lindheimeri* or much narrower; [chromosome number $n = 9$ or 18].

B. Saccate portion of keel externally puberulent with incurved hairs in upper part; plant procumbent or decumbent, deeply rooted in rocky or loose soil; leaves broadly to narrowly elliptic, obovate, or ovate, thick textured, costa prominent abaxially but other venation obscured by spongy tissue, glabrous or nearly so, distal leaves usually not markedly narrower than basal ones; upper petals with apex white or greenish white, if light rose then usually not much darker than rest of upper petal; ventrolateral

lobes of aril (0.8–)1.0–2.2 mm. long, (⅓–)½ as long as seed body to equal in length; [chromosome number $n = 18$]. ..... var. *eucosma*.

B. Saccate portion of keel glabrous or rarely externally puberulent in upper part; plant upright to procumbent, when the latter then tenaciously rooted in limestone crevices; leaves linear to elliptic or ovate, thin to thick textured, pubescent or glabrous, the distal leaves often markedly narrower than the basal ones; upper petals with apex dark rose; ventrolateral lobes of aril 0.4–1.9 mm. long, ⅕–¾ as long as seed body; [chromosome number $n = 9$]. ..... var. *parvifolia*.

Polygala lindheimeri Gray var. **eucosma** (Blake) Wendt, comb. et stat. nov.

Polygala eucosma Blake, Contr. Gray Herb. **47**: 72. 1916. TYPE: Mexico. Coahuila. Sierra Madre 40 mi. S. of Saltillo, *Ed. Palmer 2143* (GH!, K (*fide* Blake)).

This Mexican variety is most common in the Sierra Madre Oriental from southern Coahuila south to Tamaulipas and San Luis Potosí; its range also extends westward to western Zacatecas and eastern Durango, and the variety is known from one locality in Hidalgo (MAP 2). It grows on deep soils at (1525–)1800–2375 meters elevation, in woodlands of oak, oak-pinyon, or pinyon, in overgrazed grassland, and in forests of *Pinus arizonica* Engelmann.

Polygala lindheimeri Gray var. **parvifolia** Wheelock, Mem. Torrey Bot. Club **2**: 143. 1891. TYPE: United States. Arizona. Foothills of Santa Rita Mts., 25 June 1884, *C. G. Pringle s.n.* (NY (ex Herb. J. D. Smith)!, holotype; F (3 sheets)!, G!, GH!, K (*fide* Blake, 1916), MICH!, MO!, NY (2 sheets)!, US (2 sheets)!, isotypes).

Polygala tweedyi Britton ex Wheelock, *ibid.* TYPE: United States. Texas. "Tom Greene Co.," 1879, *Tweedy s.n.* (NY!, holotype; GH!, isotype).

This widespread and variable variety ranges from southeastern Arizona, southwestern New Mexico, and extreme western Texas southeastward through eastern Chihuahua, the Big Bend of Texas, and Coahuila to extreme northern Zacatecas and western Nuevo León, and from the northern Edwards Plateau of Texas northward to the Texas panhandle and southwestern Oklahoma (MAP 2). It grows in dry soils or occasionally in limestone crevices in open juniper-oak or mesquite savanna, desert grassland, and desert scrub at 350–1850 meters elevation. *Polygala lindheimeri* var. *parvifolia* intergrades with *P. lindheimeri* var. *lindheimeri* in the Big Bend region in Texas and Mexico and in northern Coahuila.

Polygala lindheimeri Gray var. **lindheimeri**.

The type variety is found in the United States only in Texas, where it ranges from the southern Edwards Plateau and southern Trans-Pecos to

the western part of South Texas; it extends southward into eastern Chihuahua, northeastern Durango, Coahuila, Nuevo León, and the Tamaulipan panhandle (MAP 2). It grows in limestone crevices and dry soil at 90–1600 meters elevation in dry juniper-oak woodland, juniper savanna, Tamaulipan thorn scrub, and desert scrub.

Polygala nudata T. S. Brandegee, Univ. Calif. Publ. Bot. **4**: 183. 1911. TYPE: Mexico. Coahuila. Sierra de la Paila, *Purpus 4762* (UC!, holotype; BM (*fide* Blake, 1916), F!, GH!, MO!, NY!, US!, isotypes).

Polygala nudata and *P. minutifolia* Rose were described in 1911 by workers on opposite coasts of the United States; the latter species had priority by several months. Blake (1916, 1924) combined these very similar taxa. However, further collections, fieldwork, and examination of the types have shown these to be distinct species; they may be distinguished by the following key.

Plants usually upright and fastigiate, often in crevices or rocky soil but rarely on vertical cliffs and then not mat-forming; stems (0.7–)0.9–1.4(–1.9) mm. in diameter (dry) in green portion; seed hairs short, projecting only 0.1–0.2(–0.4) mm. beyond seed base. ..... *P. nudata.*

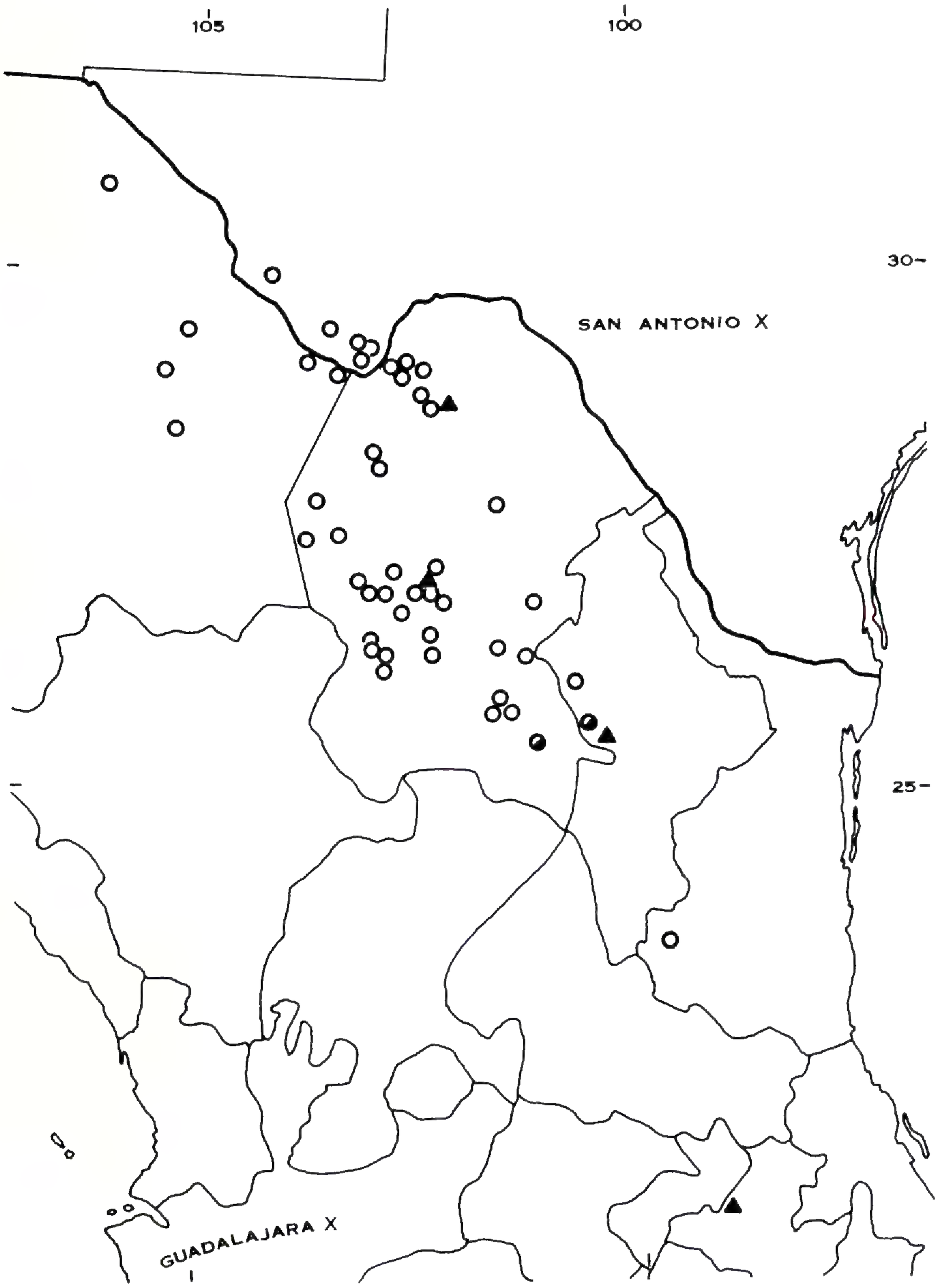
Plants confined to crevices of vertical limestone cliffs, loosely mat-forming; thickest stems 0.5–0.8(–0.9) mm. in diameter (dry) in green portion; seed hairs longer, projecting (0.3–)0.5–0.9 mm. beyond seed base. ..... *P. minutifolia.*

Polygala minutifolia is a rare species known only from the type locality near Monterrey, Mexico (*C. G. Pringle 13949* (US!, holotype; CAS!, GH!, MICH!, MO!, SMU!, isotypes)), and three other scattered localities in the mountains of eastern Mexico (MAP 3). Although it was reported from Texas by Correll and Johnston (1970), this record was probably based on material of *P. nudata*; I have seen no material of either species annotated by these authors. *Polygala nudata* is a more common species, ranging from the northern Sierra Madre Oriental of Mexico northwestward through the Chihuahuan Desert to the extreme southern portion of the Big Bend area of Texas (MAP 3). It is known in Texas and the United States from only five localities.

REPRESENTATIVE SPECIMENS. **United States.** TEXAS: Brewster Co., Blue Creek, Chisos Mts., *Cory 6999* (GH); Presidio Co., N. of Chinati Peak between Dead Horse Canyon and Pinto Canyon, 5500 ft., *Butterwick & Lott 3807B* (LL).

Polygala section MONNINOPSIS Gray, Pl. Wright. **2**: 31. 1853.

During work on a treatment of the Polygalaceae for the Chihuahuan Desert Flora (M. C. Johnston *et al.*, in preparation), the following collection of *Polygala watsonii* Chodat was discovered: United States. Texas. Brewster Co., stony limestone slopes, Old Blue, Glass Mts., 21 March 1941, *Warnock & Innes 573* (DS, GH).



MAP 3. Distribution of *Polygala minutifolia* (triangles), *P. nudata* (circles), *P. nudata* populations showing some characteristics of *P. minutifolia* (half-circles).

This represents the first known collection of this species in the United States. The above specimens had been identified as *Polygala scoparioides* Chodat, which is the closest United States relative of *P. watsonii*. The

latter species is easily distinguished from *P. scoparioides*, however, by its longer (5 mm.) wings, which distinctly exceed the capsule, and by its shorter, broader, blunt racemes. *Polygala watsonii* is a robust perennial fairly common in montane chaparral of the Chihuahuan Desert region of Mexico; it blooms profusely in the spring but only sporadically at other times. It appears to have been undercollected due to its somewhat inaccessible habitat and unusual (for that area) blooming period. *Polygala scoparioides* is a very common perennial typically found in desert flats, arroyos, and bajadas of the Chihuahuan Desert; it may bloom at any time of the year, depending on availability of moisture, but usually reaches a peak in late summer.

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REINSTATEMENT OF CLINOSTEMON (LAURACEAE)

K. KUBITZKI, H. KURZ, AND H. G. RICHTER

DURING A TAXONOMIC STUDY of the neotropical genus *Licaria* Aublet (Lauraceae) undertaken by H. K., it became apparent that *L. mahuba* (Samp.) Kosterm. and *L. maguireana* C. K. Allen occupy a very isolated position within the genus. They differ from all other species in having a pateriform (i.e., flat, saucer-shaped) cupule and also in the presence of an unusual hirsute leaf indument otherwise unknown in *Licaria*. Both species have an elongate panicle and very large obovate leaves, which have a narrow cordate base and which are clustered at the ends of the branches. However, there are some differences in details of flower structure between the two species. The stamens of *Licaria mahuba* are bent strongly downward, while those of *L. maguireana* are erect.

In this context, the findings of H. G. R., who is presently conducting a wood-anatomical study of the Lauraceae, necessitate some reconsideration of the affinities and the taxonomic position of the two species mentioned above.

XYLEM ANATOMY

Although the woods of *Licaria mahuba* and *L. maguireana* [1] show some general resemblance to *Licaria*, they have in common a number of specific anatomical features that render them distinctly different from this genus: wood surface oily to the touch; large, windowlike ("fenestriform") crossfield pitting between vessels and ray and axial parenchyma (FIGURE 1, a, b); and silica grains in ray cells, located predominantly in 2- to 5-seriate horizontal strands of shorter than average procumbent and marginal cells (FIGURE 1, c, d).

None of the above features was observed in any other *Licaria* of the nearly 50 specimens (representing 23 species) investigated except those of *L. subbullata* Kosterm., which contain silica grains in the rays but show none of the other characters. On the other hand, the combination of all three features occurs only in the genus *Mezilaurus* Kuntze ex Taubert. In terms of diagnostic value, priority has to be given to the particular arrangement of silica-bearing cells in the rays, by which specimens belonging to the genus *Mezilaurus* can easily be distinguished from all other lauraceous woods and, for that matter, from any silica-bearing woods hitherto observed and described (Amos, 1952; Ter Welle, 1976; Richter, unpubl.).

Although the two characters of oily surface and fenestriform crossfield

[1] Material investigated: *Licaria mahuba*, RBHw 15186, ex DREw 671, Brazil, Pará, Amapá; RBHw 15342, ex Uw 9085, Brazil, Pará, Amapá, Herb. MG 51845. *L. maguireana*, RBHw 14723, ex FOHw 14860, FDG 2704.

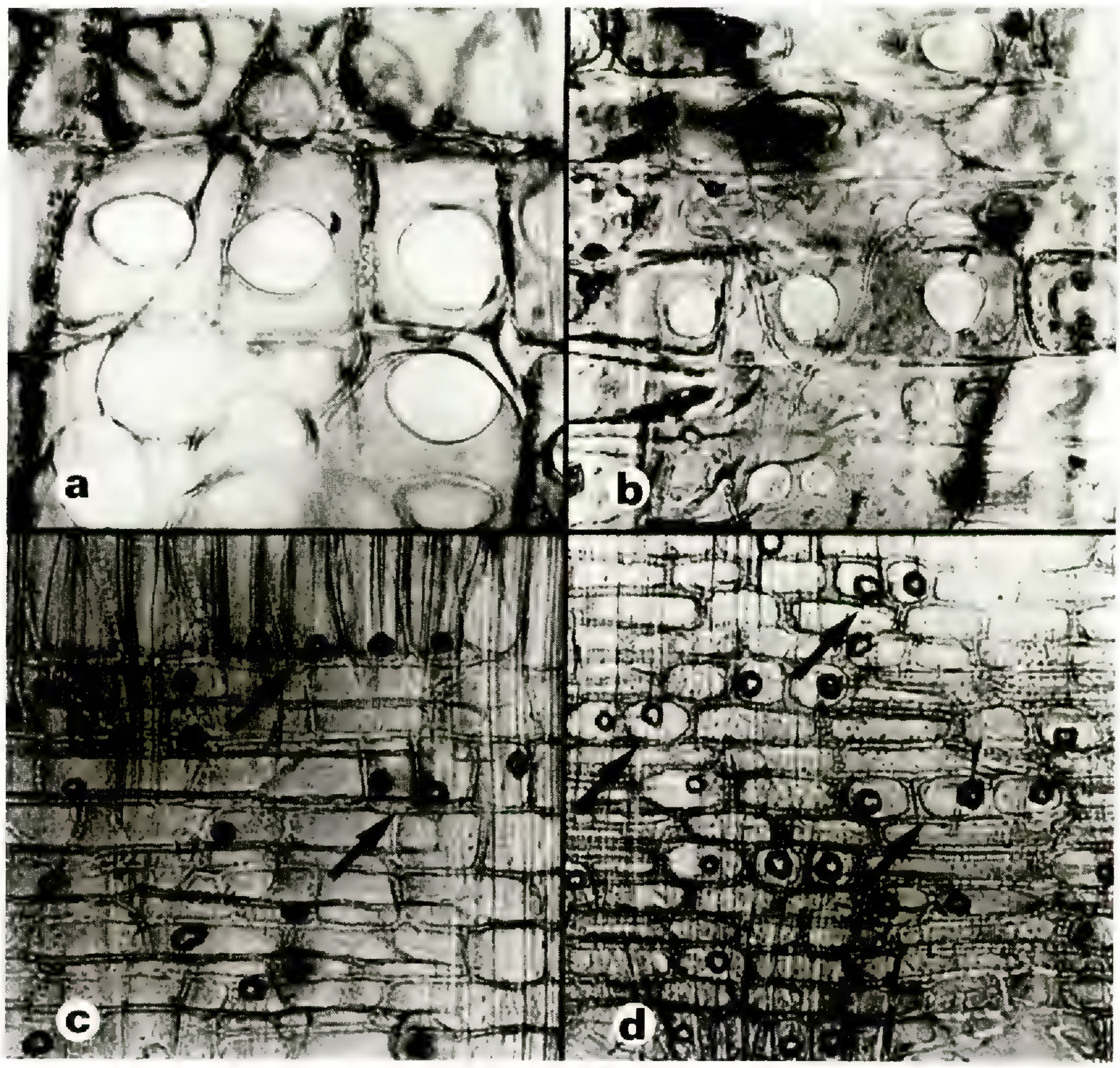

FIGURE 1. a, b, fenestriform vessel–ray pitting, × 225: a, *Clinostemon mahuba*; b, *C. maguireanum*. c, d, silica in rays, individual particles located in characteristic shorter than average cells (arrows), × 140: c, *Clinostemon mahuba*; d, *C. maguireanum*.

pitting can be observed occasionally in the Lauraceae, their simultaneous occurrence in combination with both the presence and the peculiar arrangement of silica-bearing ray cells readily identify the wood in question as either belonging to *Mezilaurus* or being very close to it.

While the wood of *Licaria maguireana* agrees closely with that of *Mezilaurus*, the wood of *L. mahuba* differs as shown in TABLE 1.

These differences, although largely of a quantitative nature, distinguish *Licaria mahuba* from *Mezilaurus* and might, in combination with other taxonomic evidence, warrant a taxonomically distinct status of this species. From a general structural point of view, however, it must remain close to *Mezilaurus*.

Wood anatomical evidence thus leads to the following conclusions: 1. The wood structure of *Licaria mahuba* and *L. maguireana* differs from that of all other species of the genus *Licaria* examined. 2. Specific structural features identify these two species as either belonging to the genus

TABLE 1. **Physical and structural properties of the wood of Licaria mahuba and Mezilaurus.**

	L. mahuba (2 specimens)	*Mezilaurus* (14 specimens from 8 species)
SPECIFIC GRAVITY (g./cm.^{3}) (air-dried specimens)	0.50–0.60	0.75–1.00
RELATION OF FIBER LUMEN (l) TO WALL THICKNESS (e)	$l \geqq 2e$	$l \ll 2e$
PORES/mm.^{2}	6–8	(11–)16(–23)
HEIGHT OF LARGEST RAYS (mm.)	1.0–2.2	(0.4–)0.7(–1.0)
COMPOSITION OF RAYS	Decidedly heterogeneous (1 (to 3) marginal row(s) of upright cells)	Homogeneous to weakly heterogeneous (1 marginal row of squarish cells)

Mezilaurus or being close to it. 3. While the wood of *L. maguireana* readily conforms to the structural pattern of *Mezilaurus*, that of *L. mahuba* occupies a more distant, yet closely related position.

TAXONOMIC EVALUATION

It is generally agreed that taxonomic entities should be based on characters that are readily observed rather than on cryptic ones. For this reason, wood anatomy can not be used as a principal tool for establishing classificatory arrangements, but it is important in testing proposed classifications. Although there is clear evidence with regard to wood structure that *Licaria mahuba* and *L. maguireana* are incorrectly placed in the genus *Licaria*, the distribution of characters of practical classificatory importance (see TABLE 2) does not suggest an obvious taxonomic solution to the problem.

The floral structure of *Licaria* is characterized by a series of reductional stages that are evidently intermediate between a more or less complete flower structure, as exemplified by *Aniba* (3 fertile stamen whorls, the innermost provided with glands), and the derived condition of *Mezilaurus*, where the androecium is represented by a single whorl of eglandulate stamens. In *Licaria* there is some variation of androecial structure between and even within species; some species conform to the pattern of *Mezilaurus*, while in others staminodia and/or stamen glands may be present. Because of this situation, the only constant diagnostic feature separating *Licaria* from *Mezilaurus* is the shape of the fruit cupule.

It is worth mentioning that, apart from *Licaria mahuba* and *L. maguireana*, there is a rather clear-cut difference between *Licaria* and *Mezi-*

TABLE 2. **Comparison of morphological characters in Licaria and Mezilaurus**

	Mezilaurus	*L. maguireana*	*L. mahuba*	Other *Licaria* spp.
CUPULE	Pateriform	Pateriform	Pateriform	Urceolate
STAMINODES (whorls I, II, IV)	Absent	Present	Present	Present in some
STAMINAL GLANDS	Absent	Absent	Present	Present in some
STAMENS	Erect	Erect	Bent downward	Erect
ARRANGEMENT OF LEAVES ON TWIGS	Clustered at end	Clustered at end	Clustered at end	Evenly distributed, rarely clustered at end
INDUMENTUM OF LOWER LEAF SURFACE	Hirsute or glabrous	Hirsute	Hirsute	Glabrous, sericeous, tomentellous, or provided with single appressed hairs

laurus, as hitherto conceived, which is reflected not only by the histological differentiation described above but also by vegetative morphology (leaves always obovate and clustered at the ends of the branches in *Mezilaurus*). Therefore, a fusion of the two genera should not be considered.

Moreover, since the shape of the cupule proves to be so important for the separation between the two genera, *Licaria mahuba* and *L. maguireana* should not be retained in *Licaria*. In addition, the flower structure of the former species, and especially the presence of exserted, downwardly bent stamens, is so unique within the Lauraceae that we propose reinstating its original generic status.

Clinostemon mahuba (Samp.) Kuhlm. & Samp. Bol. Mus. Rio de Janeiro **4**(2): 57. 1928. FIGURE 2.

Acrodiclidium mahuba Samp. Commissão Linhas Telegr. Estrat. Matto Grosso Amazonas, Publ. **56**(Annexo 5, Bot. Parte X): 14. 1917. TYPE: Brazil, Pará, Gurupá, Várzea do rio Amazonas, in flower, *Ducke MG 16538 = RB 17582* (holotype, RB; isotype, P).

Licaria mahuba (Samp.) Kosterm. Rec. Trav. Bot. Néerl. **35:** 123. 1938.

Misanteca mahuba (Samp.) Lundell, Wrightia **4:** 100. 1969.

Although the floral characters of *Licaria maguireana* are less advanced (as evidenced by the retention of staminodes), it is clearly related to species of *Mezilaurus*. Since the lack of staminodes is the most important key character for the recognition of *Mezilaurus*, the inclusion of *Licaria*

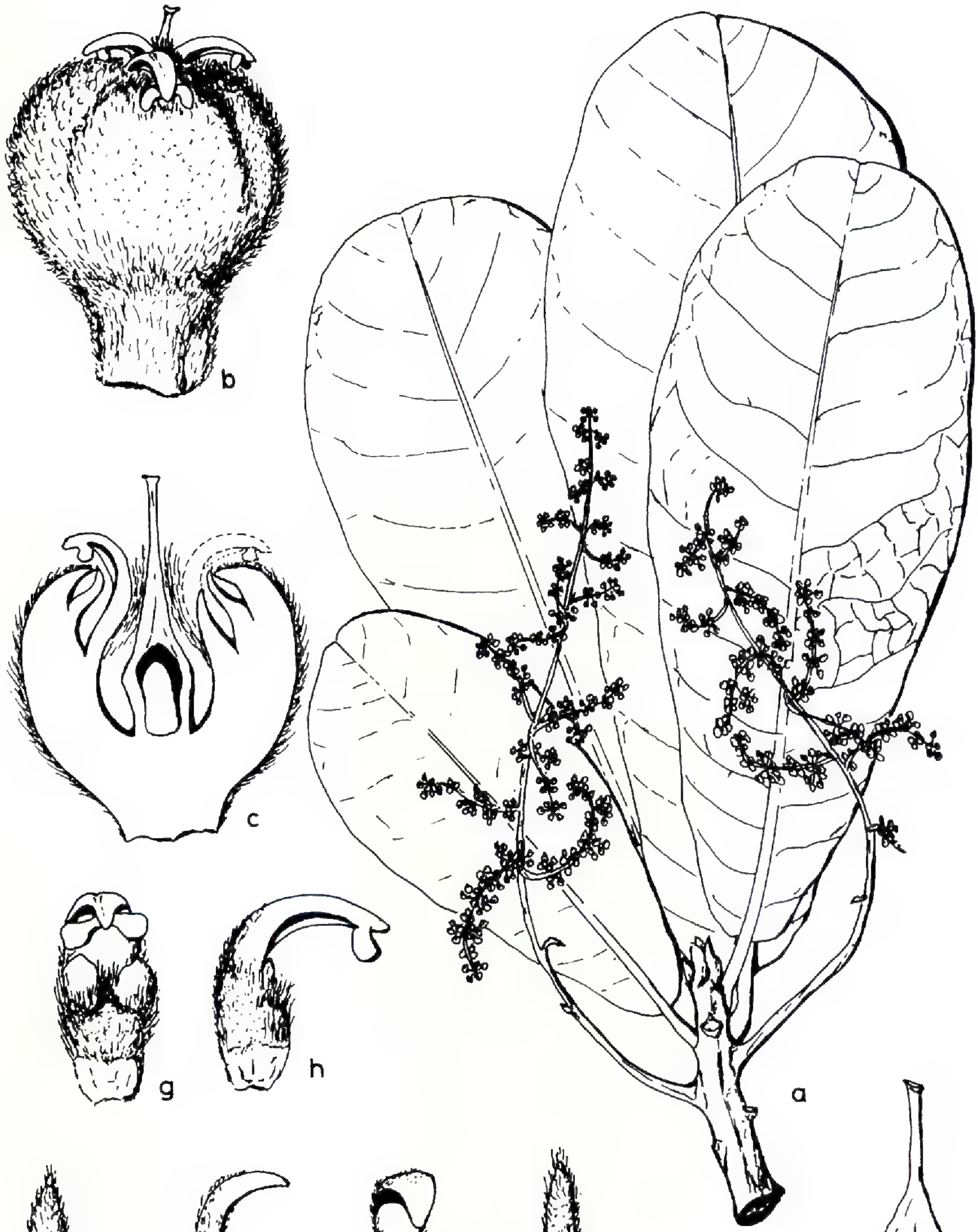

FIGURE 2. **Clinostemon mahuba** (from *Ducke 1234*): a, habit, × ¼; b, flower, × 12; c, longitudinal section of flower, × 12; d, series I staminode, side view, × 25; e, the same, dorsal view; f, series II staminode, × 25; g, stamen, dorsal view, × 25; h, the same, side view; i, series IV staminode, × 25; k, pistil, × 12.

maguireana in this genus would considerably disturb its hitherto clear definition. Now that the genus *Clinostemon* has been reinstated, including *L. maguireana* seems to be the most appropriate solution. We therefore propose the following transfer.

Clinostemon maguireanum (C. K. Allen) Kurz, comb. nov. FIGURE 3.

Licaria maguireana C. K. Allen, Bull. Torrey Bot. Club **75:** 315. 1948. TYPE: Guiana, Mazaruni Station, *Forestry Dept. Brit. Guiana 2956* (*F 220*) (holotype, NY).

Misanteca maguireana (C. K. Allen) Lundell, Wrightia **4:** 100. 1969.

The differences between the three genera under discussion can be summarized in the following key.

KEY TO THE NEOTROPICAL GENERA OF LAURACEAE WITH ONE WHORL OF BILOCELLATE STAMENS

1. Cupule urceolate, double margined. Staminodes present or absent; stamens erect, with or without glands. Leaves narrowly elliptical or ovate, rarely obovate, evenly distributed along branchlets, rarely congested near apex, the lower surface glabrous, sericeous, tomentellous, or provided with single appressed hairs, never hirsute. ..... *Licaria.*
1. Cupule pateriform. Leaves obovate or spathulate, congested near apex of branchlets, the lower surface glabrous or hirsute.
   2. Staminodes present; stamens erect or bent downward out of the flower, with or without glands. Leaves hirsute beneath. ..... *Clinostemon.*
   2. Staminodes absent; stamens erect, without glands. Leaves hirsute or glabrous beneath. ..... *Mezilaurus.*

The question of the relationship between *Licaria* and *Mezilaurus* within the Lauraceae remains to be considered. Originally, Kostermans (1938, p. 110) accepted a close affinity between the two genera, stating that the main differences were the existence of a hemispherical cupule in the former genus and of a small, pateriform enlargement of the fruit-bearing pedicel in the latter; the absence of staminal glands in *Mezilaurus* was considered of little value since *Licaria* comprehends species both with and without these glands. At the same time, Kostermans compared *Mezilaurus* with *Endiandra*, in which the fruit is attached directly to the pedicel.

In his later classification of the family, Kostermans (1957, p. 221 *et seq.*) placed more emphasis on the development of the flower tube and the fruit cupule than on any other features. Consequently, he placed *Mezilaurus* and *Endiandra* a considerable distance from *Licaria* in tribe Perseeae subtribe Beilschmiediinae. The wood-anatomical evidence shows, however, that the structural pattern of *Mezilaurus* has little in common with that of the genera assembled in Kostermans's subtribe Beilschmiediinae. This notion must inevitably lead to a reevaluation of the hierarchy of characters used in the classification of the Lauraceae and, eventually, to an improved system of classification.

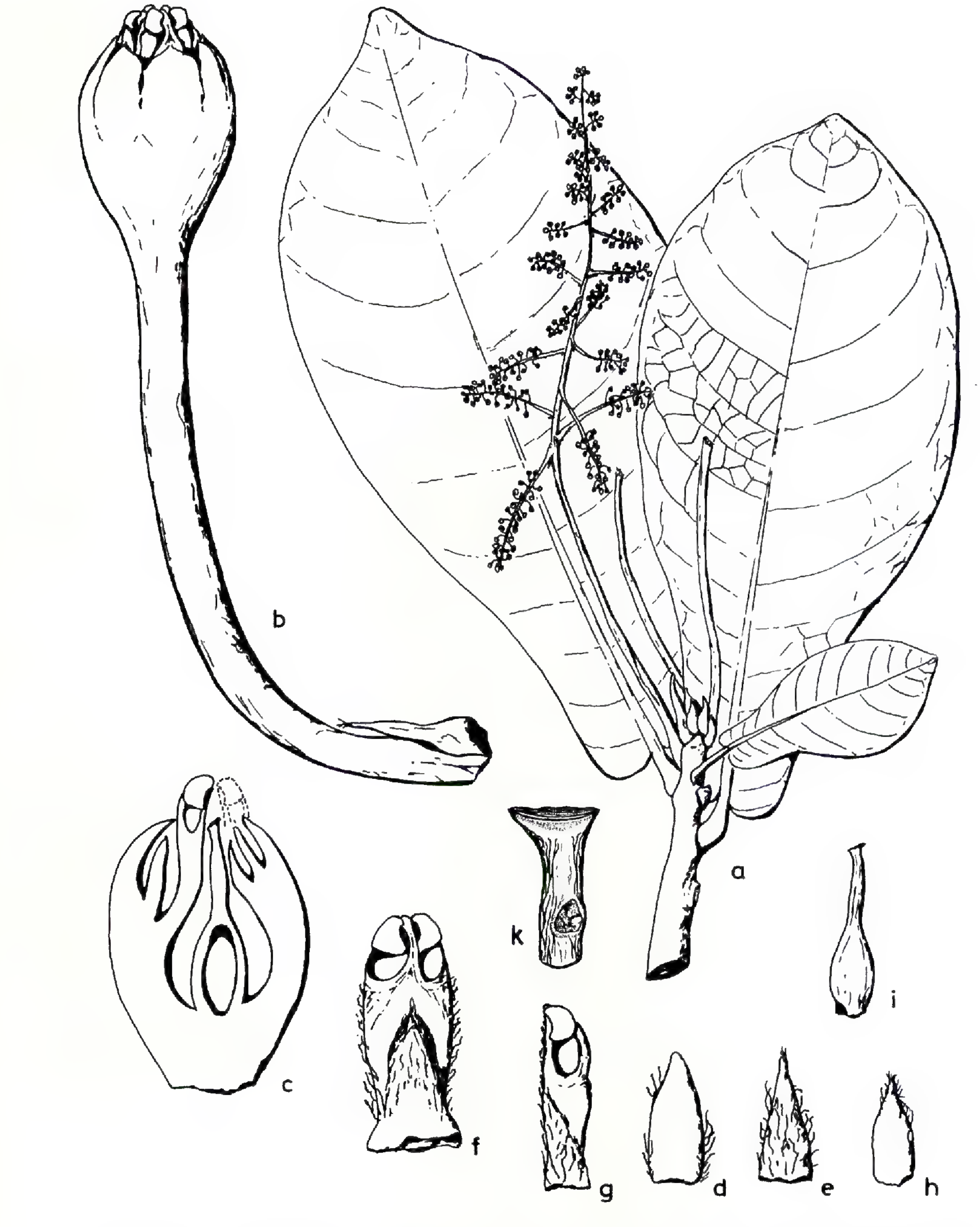

FIGURE 3. **Clinostemon maguireanum** (a–i from *Forestry Dept. Brit. Guiana 2956*, k from *INPA 15701*): a, habit, × ¼; b, flower, × 10; c, longitudinal section of flower, × 12; d, series I staminode, × 25; e, series II staminode, × 25; f, stamen, dorsal view, × 25; g, the same, side view; h, series IV staminode, × 25; i, pistil, × 12; k, cupule, × 1.5.

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FEDERAL REPUBLIC OF GERMANY

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Preliminary Announcement

Thirteenth International Botanical Congress

Sydney, Australia. 21-28th August, 1981

The Programme will consist of 12 sections — molecular, metabolic, cellular and structural, developmental, environmental, community, genetic, systematic and evolutionary, fungal, aquatic, historical, and applied botany. There will be plenary sessions, symposia, and sessions for submitted contributions (papers and posters). Chairman of the Programme Committee:—Dr. L. T. Evans.

Field Trips will include visits to arid and semi-arid regions, eucalypt forest, rain forest, heath, coastal vegetation (e.g. Great Barrier Reef, mangroves) etc., and specialist trips. Chairman of the Field Trips Committee:—Prof. L. D. Pryor.

First Circular, containing details, will be mailed in August, 1979. Send your name and full address, preferably on a postcard, to ensure your inclusion on the mailing list.

Enquiries should be sent to the Executive Secretary, Dr. W. J. Cram.

Congress address — 13th I.B.C., University of Sydney, N.S.W. 2006, Australia.

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